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University of Michigan Herbarium
Ann Arbor, Michigan
1987

CONTRIBUTIONS FROM THE UNIVERSITY OF MICHIGAN
HERBARIUM

ISSN 0091-1860

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Printed in the United States of America

Volume 16

Editor: Christiane Anderson

For information about the availability and prices of previous volumes of the *Contributions*, address the Director, University of Michigan Herbarium, North University Building, Ann Arbor, Michigan 48109-1057, U.S.A.

12 May 1987

STIGMAPHYLLON (MALPIGHIACEAE) IN MEXICO, CENTRAL AMERICA, AND THE WEST INDIES

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INTRODUCTION

Stigmaphyllon, one of the wing-fruited genera of Malpighiaceae, includes approximately 100 species and occurs from eastern Mexico and the West Indies to northern Argentina. The plants typically are vines with long-petioled, cordate to elliptical leaves and clusters of yellow flowers borne in compound inflorescences. The androecium consists of ten usually unequal stamens. In most species the three styles bear lateral appendages, the folioles, for which the genus is named. The samaras have a large dorsal wing and often smaller lateral winglets or crests.

The geographic area considered in this paper includes eastern and southern Mexico, Central America, and the West Indies excluding Trinidad and Tobago. Most of the species occur at elevations of less than 2000 m. Two exceptions are *S. pseudopuberum* and *S. cordatum*, which have been also recorded at or above 2500 m. Of the twenty-four species treated here, seven (*S. angulosum*, *S. diversifolium*, *S. emarginatum*, *S. floribundum*, *S. laciniatum*, *S. microphyllum*, *S. sagraeanum*) are endemic to the West Indies and eight (*S. adenophorum*, *S. cordatum*, *S. lindenianum*, *S. panamense*, *S. pseudopuberum*, *S. retusum*, *S. selerianum*, *S. tonduzii*) to Mexico and Central America. The remaining nine occur in South America as well. Of these, four (*S. ciliatum*, *S. ellipticum*, *S. ovatum*, *S. puberum*) are found in Mexico, Central America, and the West Indies, and three (*S. columbicum*, *S. humboldtianum*, *S. hypargyreum*) only in Costa Rica and Panama. *Stigmaphyllon adenodon* and *S. convolvulifolium* are known in our area from only a few records in the southern Lesser Antilles. For a geographical listing by country or island(s) see the appendix.

Two-thirds of our species are easily recognized. The rest have been the source of some taxonomic confusion, especially for workers who saw only few, often poor specimens. In the West Indies, the widespread *S. diversifolium* and *S. emarginatum* are bewilderingly variable in leaf shape, which is reflected by the many names published to recognize this diversity. The laminas of *S. sagraeanum* also vary but fewer synonyms exist for this species, perhaps because it is restricted to Cuba and the Bahamas.

The assemblage of superficially similar plants from Mexico and Central America for which the names *S. lindenianum* and *S. humboldtianum* have been used, often indiscriminately, proved to include five species. Two are newly described here and are known from limited areas, *S. panamense* from central Panama and the islands in the Gulf of Panama and *S. tonduzii* from northern Costa Rica. *Stigmaphyllon humboldtianum* is a species of northern Colombia and adjacent Venezuela, which extends into Darién, Panama; it is sometimes cited by the illegitimate name *S. tiliifolium*. The remaining two species have wide ranges in

Mexico and Central America and are sympatric to some extent. *Stigmaphyllon lindenianum*, whose leaves bear straight and tightly appressed hairs below, is found throughout the Atlantic lowlands from Veracruz, Mexico, to Panama; it also occurs on the Pacific side of southernmost Costa Rica (on the Osa peninsula) and of Panama. The neglected name *S. retusum* applies to plants whose leaves bear T-shaped hairs below and which occur from Veracruz and immediately adjacent Puebla, Mexico, to Nicaragua. Both *S. lindenianum* and *S. retusum* have pubescent anthers. *Stigmaphyllon humboldtianum*, the species with which *S. retusum* and to a lesser extent also *S. lindenianum* have been most often confused, also has the leaves with T-shaped hairs below but has glabrous anthers.

MORPHOLOGY

Vesture. As in all Malpighiaceae, the hairs are unicellular. If the hairs are sessile, the pubescence is termed sericeous. The hairs may also be T-shaped, consisting of a stalk up to 0.5 mm long and a crosspiece, the trabecula. If the stalk and trabecula are wavy or curled, the pubescence is termed tomentose. The mature leaves vary from glabrous to densely pubescent; if pubescent, they are always more densely hairy below than above.

Leaves. The leaf blade is commonly cordate, ovate, or elliptical, but in some species may be linear, oblong, lanceolate, rhombic, obovate, or orbicular. In *S. angulosum* the laminae are typically sinuate-lobate, while those of *S. laciniatum* are lacinate. Neither condition is found elsewhere in the genus. The laminar apex is usually acuminate and mucronate or sometimes emarginate, especially in the West Indian endemics, or sometimes caudate. The mucro is often broken off in older leaves. The base is commonly cordate or truncate or sometimes attenuate, but auriculate in *S. angulosum*, *S. ciliatum*, *S. cordatum*, and *S. selerianum*. The margin may be eglandular, or may bear scattered sessile glands, ca 0.3–0.4 mm in diameter, and/or scattered filiform glands, which are often broken off in mature leaves. The leaves of *S. ciliatum* and *S. selerianum* are ciliate. A pair of large, usually prominent glands is found at the base of the leaf or just below the base on the petiole. In *S. ovatum* the glands are flush with the surface of the petiole, and in *S. sagraeanum* and *S. microphyllum* they are usually peg- or nail-shaped. In most species the petiole of mature leaves is several centimeters long. The small stipules, less than 1.5 mm long, are triangular though sometimes narrowly so to linear. In *S. adenophorum* they consist of a prominent circular gland with a tiny membranous tip.

Inflorescence. The flowers are always borne in umbels, corymbs, or pseudoracemes (sensu Cuatrecasas 1958), either solitary or more commonly in compound inflorescences of a dichasial nature. Each flower is borne on a pedicel subtended by two bracteoles, which itself is borne on a peduncle subtended by a bract (Fig. 1c). In some species the peduncles are very short or even absent, and the pedicels then are sessile or subsessile. The bracts are eglandular, but each bracteole sometimes bears tiny, inconspicuous glands less than 0.4 mm in diameter. In *S. adenophorum* each bracteole has two prominent glands; each gland is 0.6–0.8 mm in diameter.

Perianth (Fig. 1a). The four lateral sepals each bear a pair of oblong or ovate glands; the anterior sepal is eglandular. The petals are clawed with usually orbicular to obovate or broadly elliptical limbs, whose margins vary from erose or

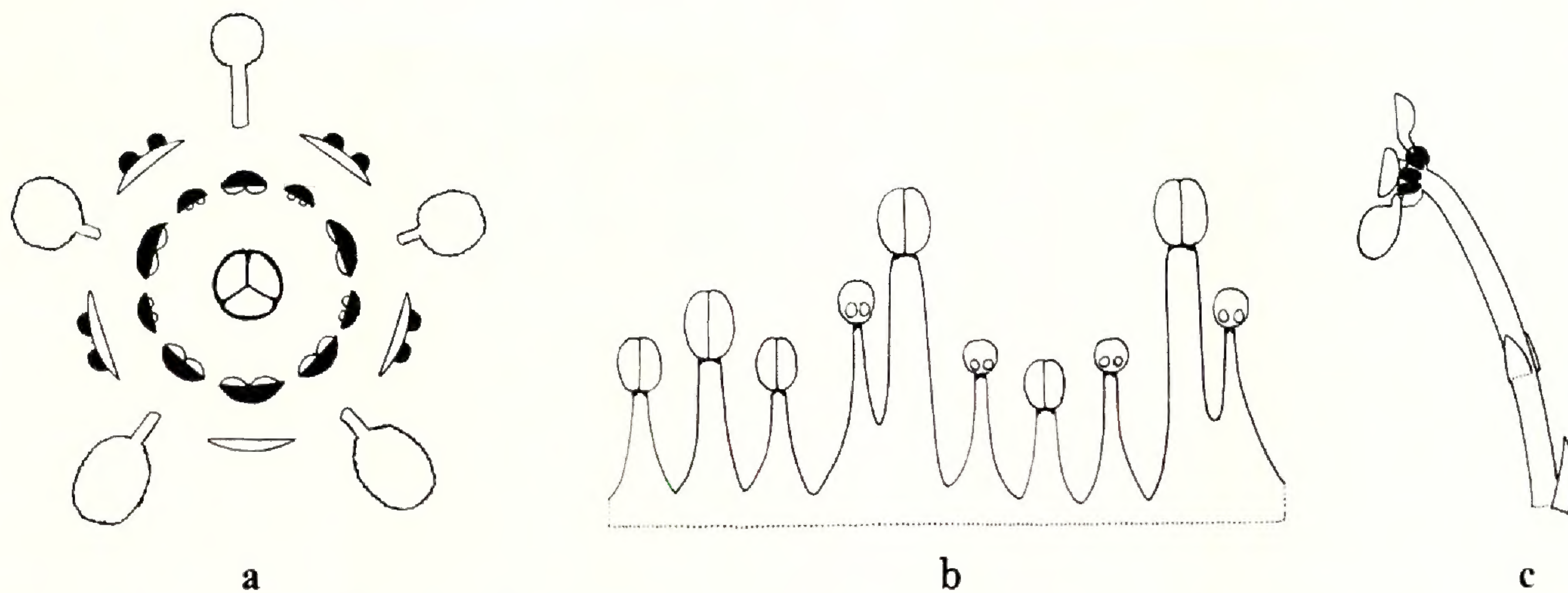


FIG. 1. Structure of flower of *Stigmaphyllon*. a. Floral diagram. b. Androecium, stamen second from left opposes anterior sepal, stamen fourth from right opposes posterior petal (the "flag"), stamens with enlarged connectives and reduced locules oppose lateral sepals. c. Typical flower borne on pedicel subtended by two bracteoles; pedicel borne on peduncle subtended by one bract.

denticulate to fimbriate. The posterior petal (the flag petal) differs from the lateral four by its stouter and longer claw, often constricted at the apex, and its smaller limb, which may also differ in its shape and margin. The posterior-lateral petals have shorter claws than the anterior-lateral petals and are generally somewhat smaller.

Androecium (Fig. 1b). In most species the ten stamens are variable in shape and size but symmetrical around a plane passing through the anterior sepal and the posterior petal. The stamens associated with the three styles, i.e., that opposite the anterior sepal and those opposite the posterior-lateral petals, are usually the largest. In most species the stamens opposite the lateral sepals have slender filaments bearing enlarged connectives with greatly reduced locules. In a few species these stamens are sterile. The anthers may be glabrous or pubescent with hairs scattered along the margins of the locules and with an apical tuft. In our area only *S. ovatum* and *S. pseudopuberum* have the androecium composed of subequal stamens.

Gynoecium. The three-carpellate ovary has three free styles. The anterior style usually differs in size and shape from the posterior two, which are mirror images of each other. The apex of the anterior style may bear a foliole on each side or may only be laterally expanded or may be linear and distally blunt or distally extended into a spur or hook. The apex of a posterior style may bear a foliole on the side toward the perianth or only a lip, or may be linear and distally blunt or distally extended into a spur or hook. In flowers in which the anterior style is foliolate, the posterior styles are also foliolate. If the anterior style is efoliolate, the posterior styles either bear folioles or may lack them as well. The presence of a foliole is apparently variable in some species. In a few individuals of *S. lindenianum* and *S. microphyllum* the folioles of the anterior style are reduced to a narrow lip or absent. In *S. sagraeanum* such variation is evident in the posterior styles. Most unusual in the genus are the canaliculate-complicate posterior styles of *S. emarginatum*. Those of *S. microphyllum* are similar but bear folioles.

Fruit. The fruit is a schizocarp, which splits into three samaras, each suspended on a carpophore. Each samara bears a large dorsal wing, thickened along

the upper (adaxial) margin, which often has a tooth at the nut. The ovoid or spherical nut may also bear small lateral winglets or spurs and/or crests or may be merely ribbed or smooth. Four species in our area differ from this pattern. In *S. ovatum* the dorsal wing is reduced to an apical crest less than 1 cm high; the carpophore is absent. The samaras of *S. ciliatum* are lenticular, i.e., laterally flattened, with the narrow dorsal wing encircling the nut. In *S. puberum* the dorsal wing also encircles the nut but tapers distally. Most unusual is the samara of *S. adenodon*; the dorsal wing is also reduced and encircles an inflated nut, whose seed is surrounded by air pockets.

The embryo of most species is ovoid, with the larger outer cotyledon often distally enfolding the smaller inner cotyledon. The embryos of *S. ciliatum* and *S. humboldtianum* are flattened. Unique in the genus is the embryo of *S. ovatum*. It consists of a large outer cotyledon, ca 12–15 mm long, folded back on itself and thus forming an open circle, and a highly reduced inner cotyledon ca 1–2 mm long.

TAXONOMY

The generic description applies to species found in Mexico, Central America, and the West Indies. Characteristics found only in exclusively South American species are not included.

Stigmaphyllon Adr. Juss. in St.-Hil., Fl. Bras. merid. 3: 48. 1832 [1833].—TYPE:

Stigmaphyllon auriculatum (Cav.) Adr. Juss.

Brachypteris Adr. Juss. in Deless., Icon. sel. 3: 20. 1837 [1838].—TYPE: *Bra-*

chyperis australis Adr. Juss., nom. superfl. [= *Stigmaphyllon paralias* Adr. Juss.].

Vines. Leaves opposite, petiolate, lamina entire or sometimes lobed (laciniate in *S. laciniatum*), usually with a pair of large glands at the base or just below the base on the petiole, stipules inconspicuous, eglandular (glandular in *S. adenophorum*), eventually deciduous. Inflorescence an umbel, corymb, or pseudoraceme, borne solitary or commonly in dichasia, compound dichasia, or small thyrses; peduncles and pedicels present, or peduncles sometimes reduced or rarely absent; bracts and bracteoles present, persistent, eglandular, or bracteoles sometimes glandular. Sepals 5, imbricate, lateral sepals biglandular, anterior sepal eglandular. Petals 5, yellow or sometimes yellow with red, clawed; posterior petal with a stouter and longer claw, commonly constricted at the apex, and a smaller limb than lateral petals. Androecium uniseriate, stamens 10, connate proximally, sometimes subequal but usually unequal, those opposite styles the largest, those opposite lateral sepals commonly with slender filaments and enlarged connectives bearing reduced locules or sometimes sterile; anthers glabrous or pubescent. Styles 3, free to the base, stigmas internal; anterior style usually different from posterior styles, erect or slightly recurved, apex with two lateral folioles or only laterally expanded or linear and distally blunt or distally extended into a spur or hook; posterior styles alike or mirror images of each other, usually lyrate or sometimes erect, apex with a lateral foliole or lip or linear and distally blunt or distally extended into a spur or hook. Ovary 3-carpellate, 3-loculate. Fruit a schizocarp of 3 samaras on a pyramidal torus and suspended on carpophores

(except in *S. ovatum*). Samara with a large dorsal wing, thickened along the upper (adaxial) margin, and small lateral winglets and/or spurs and/or crests or the nut merely ribbed or smooth, or dorsal wing sometimes greatly reduced; nut ovoid or spheroid (lenticular in *S. ciliatum*), embryo ovoid or sometimes flattened (circular in outline in *S. ovatum*). Chromosome number $n = 10$.

KEY TO FLOWERING SPECIMENS

1. Anterior style without folioles.
 2. Base of lamina auriculate.
 3. Margin of lamina eglandular; peduncles 3.3–7 mm long, ($\frac{1}{3}$ –) $\frac{1}{2}$ – $\frac{5}{8}$ as long as pedicels; posterior styles without folioles; Guatemala. *S. cordatum*.
 3. Margin of lamina ciliate; peduncles 0.5–3 mm long, up to $\frac{1}{3}$ as long as pedicels; posterior styles with folioles or at least a narrow lip; Mexico and Guatemala. *S. selerianum*.
 2. Base of lamina cordate, truncate, or attenuate.
 4. Styles subequal; stamens equal in shape, slightly unequal in size.
 5. Flowers (3–) 4 (–6) per umbel, the umbels borne solitary or in dichasia or rarely in a small thyrse; limb of lateral petals 9–12 mm in diameter; apex of styles extended into a spur 0.6–0.8 mm long; leaves sparsely sericeous below; Atlantic coastal lowlands and the West Indies. *S. ovatum*.
 5. Flowers ca 12–20 per congested pseudoraceme, the pseudoracemes usually borne in compound inflorescences, rarely solitary; limb of lateral petals ca 4–7 mm in diameter; apex of styles blunt or with a tiny spur up to 0.2 mm long; leaves sericeous to densely so below; highlands of Chiapas, Mexico, and northeastern Guatemala. *S. pseudopuberum*.
 4. Styles unequal, anterior style always shorter than the posterior two and (in most) different in shape; stamens unequal in shape and size.
 6. Peduncles absent to 9 mm long, less than $\frac{1}{3}$ as long as pedicels.
 7. Stamens opposite the lateral sepals fertile, locules always present though reduced; anthers glabrous; basal leaf glands stipitate and up to (1–) 2 mm long or subsessile or one or both glands absent; Cuba and the Bahamas. *S. sagraeanum*.
 7. Stamens opposite the lateral sepals sterile (locules absent) or rarely those opposite the anterior-lateral sepals with one or two highly reduced locules; fertile anthers commonly pubescent; basal leaf glands prominent but sessile, rarely one or both glands absent.
 8. Flowers 8–18 (–27) per umbel (sometimes a corymb or pseudoraceme), the umbels commonly borne solitary, or in dichasia or compound dichasia or rarely in a small thyrse; apex of anterior style 0.9–1.7 mm long, 0.3–1.2 mm wide, linear with a spur 0.6–1.4 mm long, or triangular to rhombic; laminas extremely variable from linear to suborbicular, 0.3–7 cm wide, sparsely sericeous or tomentose or glabrous below; Cuba and the Lesser Antilles. *S. diversifolium*.
 8. Flowers (10–) 20–25 (–45) per congested or interrupted pseudoraceme (sometimes a corymb or umbel), the pseudoracemes usually in large compound inflorescences, rarely solitary; apex of anterior style 0.6–0.7 (–1.2) mm long, 0.1–0.2 mm wide, linear with a spur 0.2–0.3 (–0.6) mm long; laminas elliptical or broadly so to oblong, sometimes suborbicular or lanceolate, 2.5–15.5 cm wide, sericeous or tomentose below, indumentum sloughed off in patches and older leaves then glabrate to glabrous below; Puerto Rico, Virgin Gorda, St. John. *S. floribundum*.
 6. Peduncles present, (1.3–) 2.5–34 mm long, more than $\frac{1}{3}$ as long as pedicels.
 9. Laminas with T-shaped hairs to tomentose below; Costa Rica. *S. columbicum*.
 9. Laminas sericeous to glabrous below.
 10. Posterior styles without folioles; West Indies except Cuba and the Bahamas. *S. emarginatum*.
 10. Posterior styles with folioles.
 11. Laminas 0.8–3.7 cm long, 0.4–1.4 cm wide, basal glands stipitate, 0.2–0.3 mm in diameter, or one or both glands absent; Cuba. *S. microphyllum*.

11. Laminas 3.5–18.5 cm long, 2–15.5 cm wide, basal glands prominent but sessile, 0.5–3.2 mm in diameter; Mexico and Central America.
12. Pedicels inflated and distally flared; flowers 3–9 (–12) per umbel or corymb; anthers glabrous; margin of lateral petals lacerate to dentate to fimbriate, teeth and fimbriae 0.4–1.2 mm long. *S. ellipticum.*
12. Pedicels terete; flowers (9–) 12–35 per umbel or corymb; anthers with full-sized locules pubescent; margin of lateral petals erose to denticulate to denticulate-fimbriate, teeth and fimbriae up to 0.2 (–0.3) mm long. *S. lindenianum.*
1. Anterior style with folioles.
 13. Anterior style and anterior stamen larger than the posterior styles and their opposing stamens; laminas sparsely to densely sericeous below.
 14. Laminas densely silvery sericeous below, epidermis not visible; flowers (15–) 20–25 per umbel; margin of petals erose or denticulate or sometimes with fimbriae up to 0.2 (–0.3) mm long. *S. hypargyreum.*
 14. Laminas sericeous to sparsely so below, epidermis visible; flowers 8–15 per umbel; margin of petals with fimbriae up to 0.6 (–0.8) mm long. *S. puberum.*
 13. Anterior style and anterior stamen smaller than the posterior styles and their opposing stamens; laminas sericeous to glabrous or with T-shaped hairs to tomentose below.
 15. Margin of lamina ciliate; pedicels inflated and flared distally. *S. ciliatum.*
 15. Margin of lamina eglandular or with scattered sessile glands and/or scattered filiform glands (these often broken off in mature leaves) but never ciliate; pedicels terete.
 16. Laminas laciniate or sinuate-lobate (usually with 5–7 lobes), or rarely ovate and then the base auriculate; Hispaniola.
 17. Laminas laciniate. *S. laciniatum.*
 17. Laminas sinuate-lobate or rarely ovate. *S. angulosum.*
 16. Laminas entire or sometimes palmately (2–) 3 (–5)-lobed, base cordate, truncate, or attenuate; Mexico, Central America, Cuba, and the Lesser Antilles.
 18. Laminas with T-shaped hairs, the stalk (0.1–) 0.2–0.3 (–0.4) mm long, to tomentose below.
 19. Bracteoles each bearing two prominent glands, each gland 0.6–0.8 mm in diameter; Costa Rica. *S. adenophorum.*
 19. Bracteoles eglandular or with tiny, inconspicuous glands less than 0.4 mm in diameter.
 20. Anthers glabrous.
 21. Limb of posterior petal 6–6.5 mm long, margin with fimbriae up to 0.4 (–0.5) mm long; margin of lateral petals (fimbriate-) denticulate, fimbriae up to 0.3 (–0.4) mm long; Panama. *S. humboldtianum.*
 21. Limb of posterior petal 6.5–8 mm long, margin erose-denticulate; margin of lateral petals erose; Costa Rica. *S. tonduzii.*
 20. Anthers pubescent.
 22. Margin of lamina with scattered sessile glands and sometimes also with scattered filiform glands (often broken off in older leaves), glands sometimes very few and margin appearing eglandular; peduncles $\frac{1}{2}$ as long as the pedicels to subequal; anterior style 1.8–3 mm long, posterior styles 2.3–3.8 (–4) mm long; Mexico to Nicaragua. *S. retusum.*
 22. Margin of lamina with stipitate, nail-like glands 0.2–0.5 mm long; peduncles subequal to $2\frac{1}{2}$ times as long as the pedicels; anterior style 2.8–3.7 mm long, posterior styles 3.5–4.7 mm long; Grenada. *S. adenodon.*
18. Laminas sericeous to glabrous or with short-stalked (up to 0.1 mm long) T-shaped hairs below.
 23. Flowers 4 in a solitary umbel; laminas 0.8–3.7 cm long, 0.4–1.4 cm wide, basal glands stipitate, 0.2–0.3 mm in diameter, or one or both glands absent; Cuba. *S. microphyllum.*
 23. Flowers (9–) 12–40 per umbel, the umbels borne in compound inflorescences; laminas 4.5–18.5 cm long, 4–15.5 cm wide, basal glands

prominent but sessile, 1–3.2 mm in diameter; Mexico, Central America, Martinique (St. Vincent?).

24. Anthers pubescent.

S. lindenianum.

24. Anthers glabrous.

25. Styles glabrous; flowers 13–ca 20 per umbel; laminas sericeous or densely so, or with short-stalked T-shaped hairs below, indumentum sloughed off in patches and older leaves often glabrate; Panama.

S. panamense.

25. Styles pubescent; flowers 20–40 per umbel, corymb, or pseudoraceme; laminas sparsely sericeous (hairs evenly distributed) to glabrous below; Martinique (St. Vincent?).

S. convolvulifolium.

KEY TO FRUITING SPECIMENS

Because most characters used to distinguish species of *Stigmaphyllon* are found in the flowers and because the size of the dorsal wing and the nature of the lateral ornamentation of the nut are often variable within the species, the key to fruiting material is less definitive than the key to flowering specimens. The choices in couplet 4, dorsal wing 1.5–3.5 cm long vs 3.5–5.4 cm long, reflect the tendency for the species so grouped to fall into two such categories, but these categories are not absolute. The highly variable *S. retusum* is keyed twice. *Stigmaphyllon adenophorum* is not known in fruit. Also excluded here is *S. columbicum*, a Colombian species recorded from Costa Rica from two flowering collections. The specimens differ somewhat from the Colombian material, and future collections, especially in fruit, may cause them to be excluded from *S. columbicum*. The samara of *S. columbicum* has a dorsal wing 3.1–4.1 cm long, without a tooth on the upper margin, and one or two rows of lateral winglets.

1. Dorsal wing flared distally, broadest at or beyond midpoint; lateral wings present, or absent and the nut smooth or bearing spurs, crests, and/or ridges.
2. Laminas laciniate or sinuate-lobate (usually with 5–7 lobes) or rarely ovate; Hispaniola.
 3. Dorsal wing 1.5–1.8 cm long; laminas laciniate. *S. laciniatum*.
 3. Dorsal wing 2.8–4.5 cm long; laminas sinuate-lobate or rarely ovate. *S. angulosum*.
2. Laminas entire, or sometimes palmately (2–) 3 (–5)-lobed in plants from Mexico and Central America.
4. Dorsal wing (3.4–) 3.5–5.4 cm long, lateral wings present or absent.
 5. Laminas with T-shaped hairs, the stalk (0.1–) 0.2–0.5 mm long, to tomentose below.
 6. Embryo flattened, ca 3 times as long as wide; upper margin of dorsal wing with a tooth; Darién, Panama. *S. humboldtianum*.
 6. Embryo ovoid, ca 2 times as long as wide; upper margin of dorsal wing with or without a tooth; Mexico to Nicaragua. *S. retusum*.
 5. Laminas sericeous or with short-stalked (up to 0.1 mm high) T-shaped hairs to glabrous below.
 7. Dorsal wing constricted at the nut to 0.3–0.4 cm wide, upper margin without a tooth; laminas densely silvery sericeous below; Panama. *S. hypargyreum*.
 7. Dorsal wing not constricted at the nut, more than 0.4 cm wide, upper margin with a tooth; laminas densely to sparsely sericeous to glabrous below.
 8. Base of lamina auriculate, margin with cilia up to 8 mm long (often broken off in older leaves); flowers 8–12 per umbel, corymb, or pseudoraceme; Oaxaca and Chiapas, Mexico. *S. selerianum*.
 8. Base of lamina truncate to cordate or attenuate, margin eglandular, or with scattered sessile glands only or also with scattered filiform glands up to 2.5 mm long (often broken off in older leaves); flowers 12–40 per umbel, corymb, or pseudoraceme.
 9. Dorsal wing 4–5.4 cm long; basal leaf glands prominent to stoutly stalked (pegshaped); highlands of Chiapas, Mexico, and northeastern Guatemala. *S. pseudopuberum*.
 9. Dorsal wing 3.4–3.8 cm long; basal leaf glands prominent but sessile; lowlands.

10. Laminas ovate or elliptical, sericeous or with short-stalked T-shaped hairs below, indumentum sloughed off in patches and older leaves then glabrate, margin eglandular or with scattered sessile glands; Panama.
S. panamense.
10. Laminas cordate or narrowly so, sparsely sericeous (hairs evenly distributed) to glabrous below, margin with scattered sessile glands and scattered filiform glands up to 2.5 mm long (often broken off in older leaves); Martinique (St. Vincent?).
S. convolvulifolium.
4. Dorsal wing 1.5–3.5 cm long, lateral wings absent, the nut smooth or bearing spurs and/or crests.
 11. Peduncles less than $\frac{1}{3}$ as long as the pedicels.
 12. Laminas glabrous below, basal glands stipitate or sometimes subsessile or one or both glands absent; dorsal wing 1.8–2.4 cm long, nut smooth; Cuba and the Bahamas.
S. sagraeanum.
 12. Laminas tomentose or sericeous to glabrous below, basal glands prominent but sessile (sometimes absent in *S. floribundum*); dorsal wing 1.5–3.2 cm long, nut smooth or bearing spurs and/or crests.
 13. Dorsal wing 1.2–2 cm long, nut smooth; flowers 8–18 (–27) per umbel, corymb, or pseudoraceme, these often borne solitary or sometimes in dichasia or compound dichasia, rarely in small thyrses; laminas 0.3–6.8 cm wide; Cuba and the Lesser Antilles.
S. diversifolium.
 13. Dorsal wing 1.8–3.2 cm long, nut smooth or bearing spurs and/or crests; flowers (10–) 20–25 (–40) per umbel, corymb, or pseudoraceme, these usually borne in large compound inflorescences, rarely solitary; laminas 2.5–15.5 cm wide; Puerto Rico, Virgin Gorda, St. John.
S. floribundum.
 11. Peduncles $\frac{1}{3}$ as long as to longer than the pedicels.
 14. Lamina with T-shaped hairs to tomentose below.
S. retusum (Mexico to Nicaragua); *S. tonduzii* (Costa Rica).
 14. Lamina sericeous to glabrous below.
 15. Base of lamina auriculate; Guatemala.
S. cordatum.
 15. Base of lamina attenuate or truncate to cordate.
 16. Basal glands of lamina stipitate or subsessile or sometimes one or both glands absent; flowers 4 in a solitary umbel; Cuba.
S. microphyllum.
 16. Basal glands of lamina prominent but sessile; flowers 3–35 per umbel, corymb, or pseudoraceme, these borne solitary or in compound inflorescences.
 17. Pedicels inflated and distally flared, 3–9 (–12) flowers per umbel (sometimes in a corymb); Mexico and Central America.
S. ellipticum.
 17. Pedicels terete, not inflated or flared; flowers (6–) 12–35 per umbel, corymb, or pseudoraceme.
 18. Dorsal wing 2–3.5 cm long; flowers in an umbel or corymb, these borne in compound inflorescences; basal leaf glands 1.2–3.2 mm in diameter; Mexico and Central America.
S. lindenianum.
 18. Dorsal wing 1.6–2.2 cm long; flowers usually in a congested or open pseudoraceme, sometimes in an umbel or rarely in a corymb, these usually borne solitary, sometimes in dichasia; basal leaf glands 0.3–1.2 mm in diameter; West Indies except Cuba and the Bahamas.
S. emarginatum.
 1. Dorsal wing broadest at the nut and tapering distally, encircling the nut, or reduced to a crest less than 1 cm high; lateral wings absent, the nut smooth or bearing prominent ribs or ridges and/or crests.
 19. Nut laterally flattened, the samara lenticular; base of lamina auriculate, margin with cilia up to 4 (–5.5) mm long.
S. ciliatum.
 19. Nut ovoid or spherical; base of lamina truncate, cordate, or attenuate, margin eglandular, or with scattered sessile glands, or with stipitate (nail-like) glands up to 0.5 mm long.
 20. Nut inflated, 12–19 mm in diameter, seed surrounded by air pockets; laminas with T-shaped hairs below, margin with stipitate (nail-like) glands; Grenada.
S. adenodon.

20. Nut not inflated, 5–11 mm in diameter, seed not surrounded by air pockets; laminas sericeous or sparsely so below, margin eglandular or with scattered sessile glands.
21. Dorsal wing reduced to an apical crest 0.4–0.9 cm high; apex of lamina acute, obtuse, or sometimes apiculate. *S. ovatum*.
21. Dorsal wing encircling the nut, 2.6–3.7 cm long measured from base of nut; apex of lamina acuminate. *S. puberum*.

Stigmaphyllon adenodon Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 288. 1840.—

TYPE: TRINIDAD, 1824, *de Schach s.n.* (holotype: K!).

Stigmaphyllon grenadense Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 26. 1900.—TYPE: TOBAGO. “In convalli fluminis Bacolit ad Cradley versus” (fide Niedenzu), *Eggers 5726* (lectotype, here designated: K!; isolectotypes: A! M! P! S!).

Stigmaphyllon kuhlmannii Pilger, Repert. Spec. Nov. Regni Veg. 42: 178. 1937.—TYPE: PERU. Solimões, Yanache, 2 Mar 1924, *Kuhlmann 1550* (holotype: RB-26279!).

Laminas 5–14.5 cm long, 3.5–15 cm wide, cordate or ovate, the smaller triangular, apex mucronate or acuminate-mucronate, base cordate or in smaller leaves truncate, glabrate to glabrous above, with T-shaped hairs below, margin with stipitate (nail-like) glands 0.2–0.5 mm long, basal glands prominent, sessile, each 1–2.4 mm in diameter; petioles 1.6–11.5 cm long; stipules triangular, eglandular. Flowers 15–30 (–35) per umbel or corymb, these borne in small thyrses or dichasia. Peduncles 3.5–14 (–17) mm long, pedicels 3.5–6 mm long, terete, peduncles subequal to or up to 2½ times as long as pedicels; bracts 0.8–1.8 (–2) mm long, broadly triangular to suboblong, bracteoles 0.6–1.2 (–1.4) mm long, ovate to oblong, eglandular. Limb of anterior-lateral petals ca 9.5–11 mm long and wide, limb of posterior-lateral petals ca 8–9 mm long and wide, limb of posterior petal ca 8–8.5 mm long and wide, all orbicular or sometimes broadly ovate, margin erose or erose-denticulate. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers pubescent. Anterior style 2.8–3.7 mm long, shorter than the posterior two, glabrous; apex 1.8–2.3 mm long, each foliole (1.1–) 1.4–1.5 mm long, (0.5–) 0.8–1.1 (–1.3) mm wide, oblong or parabolic. Posterior styles 3.5–4.7 mm long, glabrous, lyrate; folioles (1.3–) 1.8–2.5 mm long, (1.3–) 1.5–2.1 mm wide, oblong. Dorsal wing of samara encircling the nut, 3–4.4 cm high measured from base of nut, 1.1–2.1 cm wide; nut smooth or bearing shallow ridges or crests, these often interconnected, nut inflated, seed surrounded by air pockets; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Amazon basin and disjunct to the Paria Peninsula of Venezuela, Trinidad, and Tobago; in the Lesser Antilles known only from Grenada; in wet areas, along rivers and in rain forest and flooded forest; sea level to 150 m.

ADDITIONAL SPECIMENS EXAMINED. GRENADA: Tempé, *Broadway s.n.* (Feb 1905: BR; 18 Dec 1904: F, GH; Dec 1905: NY); Grand'Etang, *Smith 109* (K).

Stigmaphyllon adenodon is the only species in our area in which the nut of the samara is inflated. The locule is chambered so that the seed is surrounded by air pockets. The leaves differ from those of most of our species in that the small marginal glands are stalked and flared at the apex (nail-like).

Stigmaphyllon adenophorum C. Anderson, Syst. Bot. 11: 120. 1986.—TYPE: COSTA RICA. Puntarenas, Telecommunication Hill above the town of Golfito, ca 500 m, 16 Jul 1977, *Wilbur et al.* 22761 (holotype: MICH!; isotype: DUKE!).

Laminas 8.5–12 cm long, 4.4–7 cm wide, triangular to ovate, apex acuminate-aristate, base truncate or sometimes subattenuate, glabrate to glabrous above, with T-shaped hairs below, margin eglandular, basal glands prominent, sessile, each 1–1.6 mm in diameter, borne near the midpoint of the petiole of smaller leaves in the inflorescence; petioles 2–4.3 cm long; each stipule a prominent, circular gland, ca 0.8 mm in diameter, with a minute membranous acute tip. Flowers 16–25 per corymb, these borne in dichasia or small thyrses. Peduncles 4–8 mm long, pedicels 5.2–7.5 mm long, terete, peduncles and pedicels subequal or equal; bracts 1.2–1.6 mm long, triangular, bracteoles 1.2–1.5 mm long, ovate, each bearing two prominent glands, each gland 0.6–0.8 mm in diameter. Limb of anterior-lateral petals ca 11.5 mm long, ca 10 mm wide, limb of posterior-lateral petals ca 8–9 mm long, ca 6–7 mm wide, limb of posterior petal ca 7.5 mm long, ca 6 mm wide, all obovate, margin erose. Stamens unequal, those opposite the posterior styles the largest, those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3.7 mm long, shorter than the posterior two, glabrous; apex 1.8 mm long, each foliole ca 1.5 mm long, ca 0.8 mm wide, oblong. Posterior styles 4.2 mm long, glabrous, lyrate; each foliole 2 mm long, 2.5 mm wide, oblate. Samara not seen. Fig. 2.

Stigmaphyllon adenophorum is known only from the type. It is easily recog-

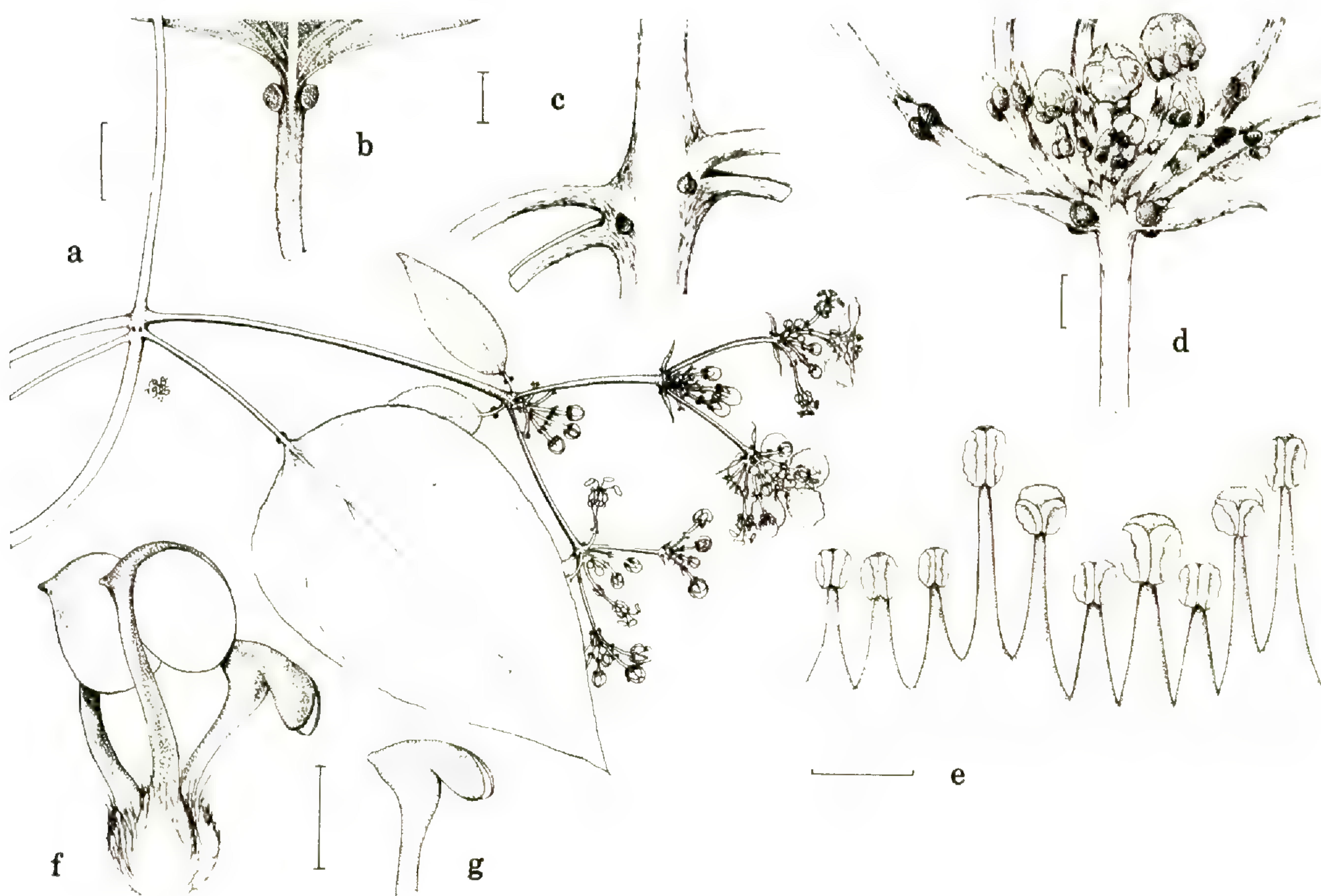


FIG. 2. *Stigmaphyllon adenophorum*. a. Flowering branch. b. Base of leaf. c. Section of stem with glandular stipules. d. Base of umbel; note glands on bracteoles. e. Androecium. f. Gynoecium. g. Distal portion of anterior style. Scale: for a, bar = 1.5 cm; for b–g, bar = 2 mm. (Based on *Wilbur et al.* 22761.)

nized by the stipules, which consist of a large prominent gland with a tiny membranous apex, and by the bracteoles, each of which bears a pair of prominent glands 0.6–0.8 mm in diameter. No other species in our area has glandular stipules or bears such glands on the bracteoles.

Stigmaphyllon angulosum (L.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 288.

1840. *Banisteria angulosa* L., Sp. pl. 1: 427. 1753. *Stigmaphyllon angulosum* f. 2. *typicum* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 12. 1900.—TYPE: *t.* 92 in Plumier, Descr. pl. Amér. 1693.

Banisteria deformis Desv. ex Hamilton, Prodr. pl. Ind. occ. 40. 1825.—TYPE: herb. Desvaux, fide Jussieu, 1843 (holotype: P?).

Stigmaphyllon angulosum f. 1. *hederifolium* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 12. 1900.—SYNTYPES: *Mayerhoff 171*, *Picarda 948*, *1358* (B, destroyed).

Laminas 4.2–16 cm long, 4.2–17 cm wide, sinuate-lobate with usually 5–7 lobes or rarely ovate, apex of each lobe apiculate, base auriculate, sericeous to glabrous above, sparsely to densely sericeous or sparsely to densely tomentose to glabrate to glabrous below, margin with filiform glands (up to 3 mm long) and/or sessile glands (up to 0.6 mm in diameter), basal glands prominent, sessile, each 1.2–1.8 mm in diameter; petioles 1.6–7.7 (–9) cm long; stipules broadly triangular, eglandular. Flowers 15–35 (–ca 40) per corymb or congested pseudoraceme, sometimes in an umbel, these borne in simple or compound dichasia or sometimes in a small thyrse or sometimes solitary. Peduncles 3.4–12 mm long, pedicels 5.5–10 mm long, terete, peduncles usually shorter than or sometimes subequal to or rarely slightly longer than the pedicels; bracts 0.7–1.5 mm long, triangular, bracteoles 0.8–1.5 mm long, triangular, eglandular. Limb of anterior-lateral petals 13–14 mm long and wide, limb of posterior-lateral petals ca 11.5–13 mm long and wide, limb of posterior petal ca 10–11 mm long and wide, all orbicular, margin irregularly dentate and/or fimbriate, especially in the distal $\frac{2}{3}$, fimbriae up to 0.4 mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 2.6–3.6 mm long, shorter than the posterior two, glabrous or with a few scattered hairs; apex 1.1–1.6 mm long, each foliole 0.7–1.4 mm long, 0.4–1.2 mm wide, narrowly to broadly parabolic. Posterior styles 3.5–4.2 mm long, glabrous or with scattered hairs, lyrate; folioles 1.3–1.6 mm long and wide, nearly square. Dorsal wing of samara 2.8–4.5 cm long, 1.2–1.8 cm wide, upper margin with a tooth; nut with a pair of lateral winglets; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Endemic to Hispaniola; pine woodlands and mixed hardwood forests, thickets, and grassy slopes; sea level to 1250 m.

REPRESENTATIVE SPECIMENS. DOMINICAN REPUBLIC. Prov. Azua, Sierra de Ocoa, San José de Ocoa, *Ekman H11880* (S, US); Barahona, *Fuertes 17* (BR, F, G, GH, MO, NY, S, US, W); prov. San Juan, Juan Santiago, *Howard & Howard 9295* (GH, MICH, NY, S, US); Monte Cristo, dist. Sabana, *Valeur 66* (G, MICH, S, US); prope Constanza, *von Türckheim 3186* (BR, G, M, NY, W).—HAITI. Massif du Nord, Port-Margot, *Ekman H2924* (G, S, US); Massif du Nord, Port-de-Paix, Haut-Piton, *Ekman H4886* (NY, S); trail to Morne Rochelois, Miragoane and vicinity, *Eyerdam 517* (GH, NY, P, US); vicinity of Mission, Fonds Varettes, *Leonard 3630* (NY, US); Nord, vicinity of Dondon, *Leonard 8633* (F, US); vicinity of Bombardopolis, *Leonard & Leonard 13411* (NY, US).

Stigmaphyllon angulosum, endemic to Hispaniola, is easily recognized by its unusual leaves, which are unique in the genus. The lamina is typically shallowly to deeply sinuate-lobate with ca 5–7 lobes, or rarely ovate, and auriculate at the base. In Hispaniola the only other species with foliolate styles is *S. puberum*, whose leaves are usually lanceolate to elliptical but never lobed. In *S. angulosum* the posterior styles and their opposing stamens are larger than the anterior style and its opposing stamen; in *S. puberum* they are smaller. *Stigmaphyllon angulosum* is probably most closely related to *S. laciniatum*, endemic to Gonâve Island and characterized by lacinate leaves.

Stigmaphyllon ciliatum (Lam.) Adr. Juss. in St.-Hil., Fl. Bras. merid. 3: 49. 1832 [1833]. *Banisteria ciliata* Lam., Encycl. 1: 369, 1783 [1785].—TYPE: BRAZIL. *Commerson s.n.* (holotype: P!; isotype?: C!).

Banisteria glauca Desf., Tabl. école bot., ed. 3, 406. 1829.—TYPE: based on living material at the Botanical Garden at Paris.

Laminas 4.3–9.5 cm long, 3.5–7.3 cm wide, broadly ovate or cordate, apex mucronate, base auriculate, glabrous or with a few scattered, appressed hairs above and below, margin with cilia up to 4–5.5 mm long, basal glands prominent, sessile, each 0.8–1.3 mm in diameter; petioles 1.6–5.1 cm long; stipules triangular, eglandular. Flowers 3–8 per umbel, these borne solitary or sometimes in dichasia. Peduncles absent to 5.3 mm long, pedicels 6–13 mm long, inflated, peduncles up to $\frac{1}{2}$ as long as pedicels; bracts 1–2 mm long, ovate to broadly so, bracteoles 0.9–1.3 mm long, almost square to broadly obovate, eglandular. Limb of anterior-lateral petals 13.5–18 mm long and wide, limb of posterior-lateral petals 11.5–16 mm long and wide, limb of posterior petal 8–11 mm long and wide, all orbicular, margin fimbriate or sometimes denticulate-fimbriate, fimbriae up to 0.5 (–0.9) mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced or with only one reduced locule or sterile; anthers glabrous. Anterior style 3.4–4.2 mm long, shorter than the posterior two, glabrous; apex 1.4–1.5 mm long, each foliole (0.9–) 1.4–1.5 mm long, 0.9–1.2 (–1.5) mm wide, parabolic or oblong. Posterior styles 4.1–5.6 mm long, glabrous, lyrate; folioles (1.3–) 1.8–2.3 mm long, 1.9–2.4 mm wide, square to parabolic. Samara lenticular, dorsal wing 2–2.5 cm long, 1.6–1.8 cm wide, encircling the nut; nut smooth; embryo flattened, ca three times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Atlantic lowlands of Belize, Guatemala, Honduras, and Nicaragua, naturalized in Barbados; most commonly in wet localities: along rivers, in mangrove or freshwater swamps, on or near beaches, and also at forest edges and roadsides; sea level to 50 m.

REPRESENTATIVE SPECIMENS. BARBADOS. Bioser Hill, St. Joseph, *Gooding* 335 (NY); Chemin de Bridgetown á Bathsheba, *Stehlé* 2946 (NY); Chemin du Turner's Hall Wood, *Stehlé* 2979 (NY).—BELIZE. Stann Creek: Gagra Creek, Commerce Bight, *Gentle* 8019 (LL, MICH, UTD); Dangriga, *Proctor* 36604 (MO); Stann Creek, *Schipp* 559 (F, G), *Schipp* 880 (F, G, GH, MICH, MO, NY, S, WIS). Toledo: Cowpen, Swarsey Branch, Monkey River, *Gentle* 4018 (A, F, MICH, MO, NY, U, UTD).—GUATEMALA. Izabal: Puerto Barrios, *Deam* 6018 (GH, MICH, US); Livingston, *Donnell Smith* 1805 (US), *Lewton* 430 (F, GH, MEXU), *von Türckheim II-1356* (US).—HONDURAS. Colón: 4.5 mi NE of Trujillo on old road to Castilla, 15°57'N, 85°54'W, *Saunders* 399 (MO, TEX). Gracias a Dios: alrededores de Puerto Lempira, *Clare* 153 (MICH).—NICARAGUA. Zelaya: vicinity of Awastara, ca 14°19'N, 83°12–13'W, *Stevens* 17741 (MO).

Stigmaphyllon ciliatum is named for its regularly and persistently ciliate leaf margins. The distinctive leaves are ovate to cordate with such deeply auriculate bases that the lobes overlap. The large flowers, borne on inflated pedicels, are aggregated in 3–8-flowered, often solitary umbels. This is the only species in our area with lenticular, i.e., laterally flattened, samaras.

This species occurs in the Atlantic coastal lowlands from Belize to Uruguay but sporadically so. It is not known from Costa Rica and Panama but may be expected there; the three records from Honduras and Nicaragua are less than ten years old. *Stigmaphyllon ciliatum* is commonly cultivated and has apparently escaped and become naturalized in Barbados.

Stigmaphyllon columbicum Nied., Verz. Vorles. Ak. Braunsberg W.–S. 1912–1913: 26. 1913.—TYPE: COLOMBIA. Cundinamarca: Anapoima, 700 m, *Triana s.n.* (lectotype, here designated: G!; isoelectotypes: COL! K!).

Laminas 5–15.5 cm long, 3.8–14.5 cm wide, cordate or narrowly so to triangular to narrowly ovate, rarely suborbicular, apex acuminate-mucronate, base cordate or sometimes truncate, glabrous above, tomentose to sparsely so below, margin with stipitate (nail-like) glands up to 0.6 mm long (Costa Rica), margin with scattered sessile glands and/or scattered filiform glands up to 1.5 mm long (Colombia), basal glands prominent, sessile, each 1–1.7 mm in diameter; petioles 1.1–7 cm long; stipules triangular to broadly so, eglandular. Flowers 20–35 (–40) per congested pseudoraceme or corymb, these borne in dichasia, compound dichasia, or small thyrses. Peduncles (5.5–) 7.5–15 mm long, pedicels 3.5–8.5 mm long, terete, peduncles ($1\frac{1}{2}$) 2– $3\frac{1}{2}$ times as long as pedicels; bracts 1.2–2.8 mm long, narrowly triangular, bracteoles 0.8–1.8 mm long, oblong or triangular, eglandular or bracteole with two inconspicuous glands up to 0.2 mm in diameter. Limb of anterior-lateral petals 10–12.5 mm long and wide, limb of posterior-lateral petals 8–10 mm long and wide, all orbicular, margin erose; limb of posterior petal ca 8–12 mm long and wide, broadly obovate to suborbicular, margin erose. Stamens unequal, those opposite the posterior styles the largest, those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3–3.7 mm long, shorter than the posterior two, glabrous; apex 1.3–1.7 mm long including a spur (0.2–) 0.3–0.5 mm long, apex 0.2–0.3 mm wide, folioles absent. Posterior styles (3.7–) 4–4.6 mm long, glabrous or rarely with a few scattered hairs, lyrate; folioles (1.6–) 2–2.6 mm long, (1.4–) 1.7–2.4 mm wide, broadly rectangular to square. In Colombian material: Dorsal wing of samara 3.1–4.1 cm long, 1–1.6 cm wide, upper margin without a tooth; nut with lateral winglets in one or two rows; embryo ovoid, ca two times as long as wide.

Phenology. Collected in Colombia throughout the year, in Costa Rica in August.

Distribution. Colombia, two collections from Costa Rica; in roadside thickets and matorrales, along rivers, at forest edge; 50–1700 m.

SPECIMENS EXAMINED. COSTA RICA. San José: ca 15.4 km S of Puriscal and 0.3 km S of Salitrales off the road to Quepos, *Almeda et al.* 3383 (CAS, F, MICH); ca 2 km beyond Salitrales towards Parritas or ca 16 km SE of Puriscal, *Wilbur et al.* 23864 (DUKE, F, MICH).

Stigmaphyllon columbicum is one of three species in Central America that have an efoliolate anterior style and foliolate posterior styles. Its leaves are tomentose to sparsely so below. The laminas of the Mexican *S. selerianum* and of the widespread *S. ellipticum* are sparsely sericeous to glabrous below. *Stigmaphyllon columbicum* might also be confused in Costa Rica with *S. adenophorum* and *S. lindenianum*, but in both all three styles bear large folioles.

This is a Colombian species, which is known in our area only from the two collections (the same population?) cited above. The Costa Rican plants differ from Colombian specimens in the glands of the leaf margin. In typical *S. columbicum*, the margins bear scattered sessile glands and/or scattered filiform glands up to 1.5 mm long (commonly broken off in mature leaves). In the Costa Rican specimens, the marginal glands are stalked, 0.2–0.6 mm long, and flared at the apex so that they appear nail-like. Additional collections from Central America, especially in fruit, need to be studied to determine whether this difference deserves taxonomic recognition.

Stigmaphyllon convolvulifolium Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840.—TYPE: FRENCH GUIANA. Cayenne, *Martius s.n.* (lectotype, here designated: P!).

Laminas 5–16 cm long, 4.5–12 cm wide, cordate, apex acuminate-mucronate, base cordate, sparsely sericeous to glabrous above and below, margin with sessile glands and filiform glands up to 2.5 mm long, basal glands prominent, sessile, each 1.1–2.4 mm in diameter; petioles 1.5–6.8 (–10.5) cm long; stipules triangular or broadly so, eglandular. Flowers 15–40 per congested pseudoraceme or corymb, these borne in dichasia, compound dichasia, or small thyrses. Peduncles 4–12.5 mm long, pedicels 3.5–9 mm long, terete, peduncles $\frac{2}{3}$ –2 times as long as pedicels; bracts 1–1.7 mm long, triangular, bracteoles 1–1.5 mm long, broadly oblong to ovate, eglandular, each bracteole with two inconspicuous glands, each up to 0.4 mm in diameter. Limb of anterior-lateral petals 11–12 mm long and wide, limb of posterior-lateral petals 8–11 mm long and wide, limb of posterior petal ca 6.5–8 mm long and wide, all orbicular, margin erose to denticulate-fimbriate, fimbriae up to 0.2 mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced or those opposite the posterior-lateral sepals with the locules only slightly reduced; anthers glabrous. Anterior style 2.8–3.3 mm long, shorter than or subequal to the posterior two, pubescent in the proximal $\frac{1}{3}$ – $\frac{1}{2}$; apex 1.5–1.9 mm long, sometimes extended beyond the folioles into a spur up to 0.2 mm long, each foliole (0.6–) 0.9–1.5 mm long, 0.7–1.5 mm wide, parabolic to broadly lunate to square. Posterior styles 3.1–4 mm long, pubescent in the proximal $\frac{1}{2}$ – $\frac{3}{4}$, lyrate; folioles 1.5–1.6 mm long, 1.6–2 mm wide, oblate to trapezoidal to square. Dorsal wing of samara 3.3–4 cm long, 1.2–1.4 cm wide, upper margin with a tooth; nut with a pair of lateral winglets only or also bearing spurs and/or crests; embryo ovoid, ca two times as long as wide.

Stigmaphyllon convolvulifolium differs from all other species in our area in that its styles are pubescent instead of glabrous. It is a South American species and has been reported only three times from the Lesser Antilles. I have only seen the collections from Martinique: *Duss 1473*, Marigot, Ste. Marie (NY); *Terrasson* in 1796 (P–JU). Niedenzu (1928) also cites *Smith & Smith 418* from St. Vincent.

Stigmaphyllon cordatum Rose in Smith, Bot. Gaz. 18: 198. 1893.—TYPE: GUATEMALA. Guatemala: 5000 ft, Mar 1892, *Heyde & Lux* 3267 (holotype: US!; isotypes: GH! NY!).

Laminas 6.1–11.5 mm long, 4.5–8.5 cm wide, cordate or narrowly so, apex acuminate or briefly so to mucronate, base auriculate, glabrous above and below, margin eglandular, basal glands prominent, sessile, each 1.1–1.7 mm in diameter; petioles 2.2–6.3 cm long; stipules triangular, eglandular. Flowers 15–20 per umbel, corymb, or pseudoraceme, these borne solitary or in dichasia. Peduncles 3.3–7 mm long, pedicels 6.5–13.5 mm long, terete, peduncles ($\frac{1}{3}$ –) $\frac{1}{2}$ – $\frac{5}{6}$ times as long as pedicels; bracts 1.5–2.3 mm long, narrowly triangular, bracteoles 1.5–1.8 mm long, narrowly triangular to sublinear, eglandular. Limb of anterior-lateral petals ca 12–13 mm long and wide, limb of posterior-lateral petals ca 11–12 mm long and wide, all orbicular, margin erose-dentate; limb of posterior petal ca 10–11 mm long, ca 8–9 mm wide, elliptical to obovate, glabrous, margin erose-dentate or sometimes also with a few fimbriae up to 0.4 mm long. Stamens unequal in size, those opposite the posterior styles the largest; anthers subequal in shape, glabrous. Anterior style 2.7–3.3 mm long, shorter than the posterior two, glabrous; apex 1.4–1.5 mm long, linear or narrowly lanceolate or expanded proximally and triangular, 0.3–0.6 mm wide, folioles absent. Posterior styles 3.5–4.2 mm long, glabrous, lyrate; apex 1.4–1.8 mm long, linear or expanded proximally on the side toward the perianth and semi-triangular, folioles absent. Dorsal wing of samara ca 3 cm long, ca 1.2 cm wide, upper margin with a tooth; nut with prominent ribs; embryo not seen.

Phenology. Collected in flower in December and February, in fruit in December and March.

Distribution. Known only from Huehuetenango and Guatemala, Guatemala; in thickets; ca 1500–2500 m.

ADDITIONAL SPECIMENS EXAMINED. GUATEMALA. Huehuetenango: Chiantla, *Hunnewell* 17152 (GH); Aguacatán, *Skutch* 1941 (F, NY, US); vicinity of Aguacatán, near the spring of San Juan, *Standley* 83145 (US), 83149 (F).

Stigmaphyllon cordatum is most similar to *S. selerianum*, endemic to Oaxaca and Chiapas, Mexico. They both have cordate, auriculate leaves. Those of *S. cordatum* have an eglandular margin and are glabrous, but those of *S. selerianum* have a ciliate margin and are sparsely sericeous to glabrate below. The peduncles of *S. cordatum* are 3.3–7 mm long and ($\frac{1}{3}$ –) $\frac{1}{2}$ – $\frac{5}{6}$ times as long as the pedicels. The bracts and bracteoles are narrowly triangular to sublinear. The peduncles of *S. selerianum* are much shorter, 0.5–3 mm long, up to $\frac{1}{3}$ as long as the pedicels, and the bracts and bracteoles are broadly triangular.

Stigmaphyllon diversifolium (H.B.K.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290. 1840. *Banisteria diversifolia* H.B.K., Nov. gen. sp. 5: 159. 1821 [1822].—TYPE: CUBA. Havana, *Humboldt & Bonpland* s.n. (holotype: P-HBK!).

Banisteria ledifolia H.B.K., Nov. gen. sp. 5: 159. 1821 [1822]. *Stigmaphyllon ledifolium* (H.B.K.) Small, N. Amer. fl. 25(2): 141. 1910.—TYPE: CUBA. Havana, *Humboldt & Bonpland* s.n. (holotype: P-HBK!).

- Stigmaphyllon lineare* Wright ex Griseb., Catal. pl. cub. 43. 1866.—TYPE: CUBA. Cabo del Rey, *Wright 2156* (holotype: GH!; isotypes: G! MO! P!).
- Stigmaphyllon sericeum* Wright ex Griseb., Catal. pl. cub. 43. 1866. *Stigmaphyllon diversifolium* β *sericeum* (Wright ex Griseb.) Gómez, Anales Soc. Esp. Hist. Nat. 19: 232. 1890.—TYPE: CUBA. Río Toro, *Wright 2155* (holotype: GH!; isotypes: G! P!).
- Stigmaphyllon rhombifolium* Wright in Sauv., Anales Acad. Ci. Méd. Habana 5: 244. 1868.—TYPE: CUBA. “Potreros de D. Francisco Sauvalle. Bahía Honda y Santa Cruz de los Pinos,” *Wright 3521* (holotype: HAB?; isotypes: NY! P! S! US!).
- Stigmaphyllon cordifolium* Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 8. 1899.—TYPE: MARTINIQUE, fide C. D. Adams, pers. comm., (labeled “Fl. trinitatis”), *Sieber 135* (lectotype, here designated: G!; isotypes: F! GH! M! MO! W!).

Laminas 1.8–14.7 cm long, 0.3–6.8 cm wide, extremely variable: linear to lanceolate to elliptical to ovate to obovate to rhombic to orbicular, apex mucronate or mucronate-emarginate, base truncate to cordate or acute, tomentose or sparsely so or sericeous to glabrous above and below, margin eglandular, basal glands prominent, sessile, each 0.3–1 (–1.4) mm in diameter or sometimes absent; petioles 1–13.5 cm long; stipules narrowly triangular to linear, eglandular. Flowers 8–18 (–27) per umbel, or sometimes in a corymb or pseudoraceme, these often borne solitary, sometimes in dichasia or compound dichasia, rarely in small thyrses. Peduncles absent to 3.5 mm long, pedicels 7–22 mm long, terete, peduncles if present always much shorter than pedicels; bracts 0.9–2.2 mm long, narrowly triangular, bracteoles 0.5–1.1 mm long, narrowly triangular, eglandular. Limb of lateral petals 7.5–11 mm long and wide, limb of the posterior petal (6.5–) 7.8–8.5 (–9.5) mm long and wide, all orbicular, margin erose. Stamens unequal, those opposite the posterior styles the largest, anthers opposite the lateral sepals sterile or sometimes those opposite the anterior-lateral sepals with the connective enlarged and with one or two reduced locules; fertile anthers pubescent or sometimes glabrous. Anterior style 1.5–3.5 mm long, shorter than the posterior two, glabrous or sometimes with a few hairs near the stigma; apex 0.9–1.7 mm long including a spur 0.6–1.4 mm long, linear or expanded proximally and triangular to rhombic, 0.3–1.2 mm wide, folioles absent. Posterior styles 2.1–5.8 mm long, glabrous or sometimes with a few hairs near the stigma, lyrate; apex 0.4–0.7 mm long including a spur up to 0.2 mm long or blunt, ca 0.1 mm wide, folioles absent. Dorsal wing of samara 1.5–2 cm long, 0.5–1 (–1.3) cm wide, upper margin with a tooth; nut smooth or with prominent ribs; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Cuba and the Lesser Antilles south to Martinique; on limestone and serpentine outcrops, in coastal thickets, pastures, and palm barrens; sea level to 500 m.

REPRESENTATIVE SPECIMENS. CUBA. Camagüey: savanna S of Sierra Cubitas, *Shafer 514* (NY); Camagüey to Santayana, *Britton 2355* (NY). Havana: near Havana, *Shafer 85* (CM, NY); Cojimar, *Killip 13819* (US). Mantanzas: near mouth of the Bueyvaca, *Britton & Wilson 60* (NY); vicinity of Mantanzas, gorge of the Yunuri, *Britton et al. 247* (CM, F, NY). Oriente: vicinity of Guantánamo, *Britton 1897* (NY); Río Seboruco to falls of Río Mayari, *Shafer 3689* (NY, US); Ensenada de Mora, *Britton et al. 13032* (NY, US). Pinar del Río: Corrientes Bay, *Britton & Cowell 9897* (NY); Sierra de

Anafe, *Britton et al.* 10340 (NY). Santa Clara: Ciento Viejo Arroyo, 12½ km E of Santa Clara, *Howard* 5088 (GH, NY); Limones, Soledad Cienfuegos, *Jack* 5873 (A, CAS, F, LE, S, US). Isla de Pinos: Vivijagua, *Britton et al.* 15025 (NY). Without definite locality: *Wright* 2153 (G, GOET, LE, MO, NY, P, S, US, W); *Wright* 2154 (G, GH, GOET *p.p.*, MO, P).—ANGUILLA. *Boldingh* 3513 (U), *Howard & Kellogg* 19080 (MICH), *LeGallo* 2499 (NY), *Proctor* 18581 (A).—ST. MARTIN. *Arnoldo* 3433 (U), *Boldingh* 3286 (U).—ST. BARTHÉLEMY. *LeGallo* 2212 (A).—BARBUDA. *Box* 684 (MO, US), *Cowan* 1648 (GH, NY, US), *Howard* 18518 (A).—ST. KITTS. *Barneby* 17782 (MICH, NY), *Britton & Cowell* 750 (NY, US).—ANTIGUA. *Rose et al.* 3275 (NY, US), *Sauer* 2087 (F), *Smith* 10494 (A, NY, S, US).—MONTSERRAT. *Proctor* 19193 (A), *Shafer* 616 (F, NY, US).—GUADELOUPE. *Duss* 2413 (F, GH, MO, NY, US), *Questel* 1470 (P, US).—LES SAINTES. *Stehlé* 1691 (NY).—DOMINICA. *Beard* 1459 (GH, NY, S, US), *Stern & Wasshausen* 2539 (US), *Wilbur* 7641 (F, LL, MICH, MO, TEX).—MARTINIQUE. *Duss* 437 (F, NY, US), *Duss* 438 (F, NY).

Stigmaphyllon diversifolium is most reliably distinguished by features of the flowers and inflorescence. The anthers opposite the lateral sepals are sterile (or sometimes those opposite the anterior-lateral sepals have one or rarely two greatly reduced locules), and the styles all lack folioles. Each posterior style curves around its opposing stamen; when these styles are very long, as in plants from the Lesser Antilles, they are conspicuously curled distally. The flowers, usually fewer than 20, are borne in solitary umbels or in dichasia. The pedicels are either sessile or borne on very short peduncles (up to 3.5 mm long).

This species is well named for its leaves, which are highly variable in size, shape, and vesture. The extremes in variation have been recognized as separate taxa. Because they are all linked by intermediates and are conservative in the flower and inflorescence characters, they are not recognized here. The most distinctive segregate is *S. cordifolium*, established by Niedenzu for plants from the Virgin Islands and the Lesser Antilles. These plants tend to be less variable than the Cuban specimens. They usually have ovate láminas which are pubescent below even at maturity, larger leaf glands, and somewhat longer styles; however, specimens similar to the Cuban plants also occur. All specimens recorded from Anguilla and St. Martin have linear leaves; in *Stern & Wasshausen* 2539 from Dominica the leaves vary from broadly elliptical to suborbicular.

Stigmaphyllon diversifolium is most often confused with *S. emarginatum*, a species found throughout the West Indies except in Cuba, the Bahamas, and Dominica. It differs from *S. diversifolium* in that its anthers are all fertile and in its unusual posterior styles, which are canaliculate-complicate and erect (never curved or curled around the opposing stamen). The flowers are most commonly arranged in solitary pseudoracemes; the peduncles are ½ to equally as long as the pedicels. The leaves and stems are most often glabrous at maturity. *Stigmaphyllon diversifolium* is most similar to the Puerto Rican *S. floribundum*; see that species.

Stigmaphyllon ellipticum (H.B.K.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290. 1840. *Banisteria elliptica* H.B.K., Nov. gen. sp. 5: 161. 1821 [1822].—TYPE: ECUADOR. Loja: "Loxa" [Loja], *Humboldt & Bonpland s.n.* (holotype: P-HBK!).

Banisteria mucronata DC., Prodr. 1: 589. 1824. *Stigmaphyllon mucronatum* (DC.) Adr. Juss., Arch. Mus. Hist. Nat. Paris 3: 377. 1843. *Stigmaphyllon mucronatum* var. γ *typicum* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 4. 1900. *Stigmaphyllon ellipticum* var. γ *typicum* (Nied.) Nied., Pflanzenreich IV. 141(2): 500. 1928.—TYPE: "... in Nova-Hispania?," collector unknown (holotype: G-DC, photo: F! MICH!).

- Banisteria ternata* DC., Prodr. 1: 591. 1824. *Stigmaphyllon ternatum* (DC.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289. 1840. *Stigmaphyllon mucronatum* var. δ *ternatum* (DC.) Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 4. 1900. *Stigmaphyllon ellipticum* var. δ *ternatum* (DC.) Nied., Pflanzenreich IV. 141(2): 501. 1928.—TYPE: Sessé and Mociño plate, number 6331.1667 in the Torner Collection of Sessé and Mociño Biological Illustrations at the Hunt Institute for Botanical Documentation.
- Banisteria billbergiana* Beurl., Kongl. Vetensk. Akad. Handl. 1854: 116. 1854.—TYPE: PANAMA. Colón: "Porto Bello [Portobelo], ad litora insulae Manzinella [Manzanillo]," *Billberg* 285 (holotype: S!; isotype: S!).
- Stigmaphyllon mucronatum* var. α . *nicaraguense* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 4. 1900. *Stigmaphyllon ellipticum* var. α . *nicaraguense* (Nied.) Nied., Pflanzenreich IV. 141(2): 500. 1928.—TYPE: NICARAGUA. Matagalpa: 800 m, *Rothschuh* 643 (holotype: B, destroyed).
- Stigmaphyllon mucronatum* var. β . *intermedium* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 4. 1900. *Stigmaphyllon ellipticum* var. β . *intermedium* (Nied.) Nied., Pflanzenreich IV. 141(2): 500. 1928.—TYPE: PANAMA. "Río Bayono [Bayano]," Mar 1858, *Wagner s.n.* (*Fasc. 11*) (lectotype, here designated: M!).

Laminas 3.5–15.2 cm long, 2–8.6 cm wide, narrowly to broadly elliptical, sometimes lanceolate to ovate, rarely suborbicular, apex mucronate to attenuate, rarely caudate, base truncate to cordate, sometimes attenuate, (very sparsely sericeous to) glabrate to glabrous above and below, margin eglandular, basal glands prominent, sessile, each 0.5–2 mm in diameter; petioles 0.6–2.8 cm long; stipules triangular, eglandular. Flowers 3–9 (–12) per umbel or sometimes a corymb, these borne solitary or in dichasia or small thyrses. Peduncles (1.5–) 2.5–34 mm long, pedicels 2–13 mm long, inflated, peduncles $\frac{1}{2}$ –5 times as long as pedicels; bracts 0.9–2 mm long, triangular, bracteoles 0.7–1.8 mm long, oblong to ovate, eglandular. Limb of anterior-lateral petals (11–) 12–17 mm long, 12–17 mm wide, limb of posterior-lateral petals 10–16 mm long, 12–16.5 mm wide, all orbicular; limb of posterior petal (8–) 11–14.5 mm long, (7–) 10.5–14 mm wide, obovate to broadly elliptical to orbicular; margin of all petals lacerate, lacerate-dentate, lacerate-fimbriate, dentate-fimbriate, or fimbriate, teeth and fimbriae 0.4–1.2 mm long. Stamens unequal, those opposite the lateral sepals the longest and with the connective enlarged and the locules reduced, rarely anthers of those opposite the posterior-lateral sepals sterile; anthers glabrous. Anterior style (2.3–) 2.7–3.8 mm long, shorter than or sometimes subequal to the posterior two, glabrous; apex 1–1.5 mm long, the distal $\frac{1}{2}$ – $\frac{3}{4}$ (– $\frac{4}{5}$) elliptically to ovately to suborbicularly (rarely triangularly) expanded, (0.3–) 0.4–0.7 (–0.8) mm wide, folioles absent. Posterior styles (2.3–) 2.6–3.6 mm long, glabrous, erect; folioles 0.9–1.5 mm long, (0.5–) 0.7–1 mm wide, lunate to broadly so. Dorsal wing of samara 2.1–3.5 cm long, 0.8–1.3 cm wide, upper margin usually with a tooth; nut sometimes with a pair of lateral winglets, commonly only bearing spurs and/or crests or only prominently ribbed; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. From southeastern Mexico to northern South America; in evergreen, deciduous, rain, thorn, and pine-oak forest, in second growth, thickets, matorral, and at roadsides and edges of beaches; sea level to 2200 m.

REPRESENTATIVE SPECIMENS. MEXICO. Campeche: Km 71, camino Escárcega a Candelaria, *Chavelas P. et al. ES-372* (MEXU, MICH); Tuxpeña, *Lundell 975* (A, CAS, F, GH, MICH, MO, NY, US, WIS). Chiapas: 9 mi E of Cintalapa on Mex hwy 190, *Anderson & Laskowski 4221* (ENCB, GH, MICH, MO, NY); Mpio Villa Flores, 14 km N of Villa Flores along rd to Tuxtla Gutiérrez, *Breedlove 24605* (DS, MEXU, MICH, MO, NY); Mpio Solosuchiapa, 2–4 km below Ixhuatán along rd to Pichucalco, *Breedlove 34869* (DS, MEXU, MICH). Oaxaca: gorge of Río Malatengo, *Alexander 150* (MEXU, MICH, NY); dist. Cuicatlán, de Palapa a la Raya, *Conzatti 3789* (MEXU, US); Chivela, *Mell 2251* (NY, US). Quintana Roo: Coba, at Lake Coba, *Lundell & Lundell 7668* (MICH, UTD); a 6 km al N de La Unión, *Téllez 1656* (CAS, MEXU, MO). Tabasco: a 2 km N del camino 25 y a 5.2 km al W de la W-O, Balancan, *Novelo et al. 103* (CAS, MEXU, MO). Tamaulipas: irrigation ditch 3 mi S of Ciudad Mante, *Hill 39* (TEX). Veracruz: Laguna Encantada, 6 km al N de San Andrés Tuxtla, *Calzada 950* (CAS, F, MEXU, MO); Atoyac, *Matuda 1470* (A, GH, MEXU, MICH, MO, US); Mpio Dos Ríos, Cerro Gordo, cerca del Salto del Río Grande, *Ventura A. 2624* (CAS, DS, ENCB, F, MICH, NY, P, TEX, US). Yucatán: Izamal, 1888, *Gaumer s.n.* (F).—BELIZE. El Cayo: Vaca, *Gentle 2490* (MEXU, MICH, TEX). Toledo: riverbank of Río Grande, *Gentle 4816* (LL, MICH, UTD). Stann Creek: Savannah Forest Station, 16°34'N, 88°20'W, *Hunt 356* (F, US, UTD).—GUATEMALA: Alta Verapaz: along Río Sebol, downstream from Carizal, *Steyermark 45778* (F, LL). Chiquimula: around Ipala, *Steyermark 30363* (F). El Progreso: Fiscal, *Deam 6172* (F, GH, MICH, US). Escuintla: Escuintla, *Harmon & Dwyer 2985* (F, GH, MO). Huehuetenango: near El Reposo, ca 8 km from Mex. frontier, *Williams et al. 41130* (F). Izabal: between Los Amates and Izabal, *Kellerman 7255* (US); near Quiriguá, *Standley 72347* (F). Jutiapa: vic. of Jutiapa, *Standley 74973* (F, US). Petén: Guayacan, bordering Laguna Guayacan, *Contreras 7371* (LL, UTD); Parque Nacional de Tikal, km 59 del camino de El Renate, *Tún Ortiz 373* (F, MO, NY, US). Santa Rosa: near Cuilapa, *Standley 73536* (F). Suchitepéquez: along Río Madre Vieja, above Patutul, *Standley 62209* (F). Zacapa: Gualan, *Kellerman 5733* (LL, US); Sierra de las Minas, vic. of Río Hondo, *Steyermark 29379* (F).—HONDURAS. Atlantida: vaguada del Río Cangrejal, 20 km SE de La Ceiba, *Nelson et al. 3390* (MO). Cholutea: Marcovia, 20 km de Cholutea, *Argeñal 171* (MICH). Comayagua: cerca de La Libertad, matorrales del Río Frío, *Molina R. 7027* (F, GH, US). Copán: 1 mi W of Ruinas Copán, *Molina R. & Molina 30851* (F). Cortés: nacimiento del Río Lindo, *Molina R. 5680* (F). El Paraíso: matorral del Río Tenpasenti, cerca del pueblo Tenpasenti, *Molina R. 11917* (F, G, NY, US). Gracias a Dios: arroyada del Río Dursuna, 70 km al O de Puerto Lempira, 15°00'N, 84°13'W, *Nelson 798* (MO). Morazán: near Suyapa, along quebrada Suyapa, *Molina R. 702* (F, GH, MEXU). Santa Bárbara: San Pedro Sula, *Thieme 5168* (GH, US).—EL SALVADOR: Ahuachapán: vic. of Ahuachapán, *Standley 19847* (GH, NY, US). La Libertad: vic. of San Tecla, *Standley 23013* (GH, S, US). La Unión: vic. of La Unión, *Standley 20832* (US). San Salvador: vic. of Tonacatepeque, *Standley 19468* (GH, MO, S, US). Santa Ana: vic. of Metapán, *Standley & Padilla V. 3207* (F). Sonsonate: vic. of Acajutla, *Standley 21973* (GH, US).—NICARAGUA: Boaco: Las Pitas, 12°28'N, 85°35'W, *Moreno 10653* (MO). Chontales: rd from Juigalpa NE toward La Libertad, ca 17.4 km NE of Río Mayales, ca 12°12'N, 85°17'W, *Stevens 4188* (MICH). Jinotega: "El Recreo," 4 km al N de Sta Gertrudis, 13°13'N, 85°53'W, *Moreno 7918* (MICH). Madriz: ca 5 km SW of San Juan del Río Coco on rd to Telpaneca, ca 13°31'N, 86°11'W, *Stevens 17672* (MICH). Masaya: Parque Nacional Volcán Masaya, on N flank of Volcán Santiago, *Neill 2844* (MICH, MO). Matagalpa: E side of Río Tuma between bridge and Río Yasica, ca 13°03'N, 85°44'W, *Stevens 19188* (MO). Nueva Segovia: a 6 km del Jicaro, carretera a Murra, 13°44'N, 86°05'W, *Moreno 8308* (MICH). Río San Juan: 10 km al SSE de San Miguelito, sobre la carretera a San Carlos, *Sandino 5038* (MO). Zelaya: Monkey Point, 11°36'N, 83°40'W, *Moreno 12359* (MO); ca 2.5 km NW of Rama, ca 12°10'N, 84°14'W, *Stevens 17465* (MO).—COSTA RICA. Alajuela: Canton Atenas, Angeles de Atenas, barranca del Río Grande, *Smith 2446* (GH, US). Guanacaste: ca 10–20 km NE of Liberia on Camino Santa María, *Utley & Utley 3114* (DUKE, MICH). Limón: vic. of Westfalia, S of Limón, *Almeda et al. 3225* (CAS, MICH). Puntarenas: Cabo Blanco Nature Reserve, S tip of Nicoya peninsula, 9°35'N, 85°6'W, *Burger & Liesner 6649* (F); near Rincón de Osa, *Liesner 2214* (MO). San José: from Palmital to San Ignacio, *Khan et al. 193* (MICH).—PANAMA: Bocas del Toro: Isla Colón, vic. of Chiriquí Lagoon, *von Wedel 2828* (GH, MICH, MO, NY). Canal Zone: near Gatún Lake, *Croat 4707* (F, MO, NY); near Salamanca Hydrographic Station, *Dodge et al. 16966* (G, MO, S, U); Barro Colorado Island, *Foster 1320* (F, GH, MICH). Chiriquí: Volcán dist. near Las Lagunas, *D'Arcy 10054* (MICH, MO, NY, U); Burica peninsula, N of San Felix, *Mori & Kallunki 6024* (MICH, MO, NY, US). Coclé: vic. of El Valle, *Allen 1777* (MO). Colón: María Chiquita, *Ebinger 434* (F, GH, MO). Darién: Río Chucunaque, above Yaviza, *Gentry 13478* (COL, F, MICH, MO). Herrera: above Chapo de las Minas, *Folsom et al. 7005* (MO, MICH). Los Santos: Los Teretos, *Dwyer 2438* (MO, US). Panamá: Cerro Jefe, *D'Arcy 9733* (LL, MO, P, TEX). San Blas: Ailigandí,

Dwyer 6858 (MO). Veraguas: between Santa Fe and Escuela Agrícola Alto Piedras, Croat & Folsom 33836 (CAS, MO, TEX).

Stigmaphyllon ellipticum is very common throughout the Mexican and Central American lowlands and is easily distinguished from all other species. The leaves are usually elliptical, glabrate to glabrous, and have rather short petioles (less than 3 cm long). The flowers are large and clustered in few-flowered umbels. The inflated pedicels are usually shorter than the peduncles in plants from Mexico to Costa Rica; in plants from Panama they are commonly subequal. The anterior style lacks folioles but is somewhat laterally expanded; the posterior styles bear lunate folioles.

Stigmaphyllon emarginatum (Cav.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290. 1840. *Banisteria emarginata* Cav., Diss. 9: 425. 1790.—TYPE: Plate 249 in Cav., Diss. 9. 1790 (lectotype, designated by Niedenzu, 1899).

Banisteria periplocifolia Desf. ex DC., Prodr. 1: 589. 1824. *Stigmaphyllon periplocifolium* (Desf. ex DC.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290. 1840.—TYPE: PUERTO RICO. Bertero s.n. (G-DC, microfiche MICH!).

Triopteris lingulata Poiret in Lam., Encycl. 8: 104. 1808. *Stigmaphyllon lingulatum* (Poiret) Small, N. Amer. fl. 25(2): 140. 1910.—TYPE: DOMINICAN REPUBLIC. "de St. domingue," collector unknown (holotype: P-LAM!).

Banisteria umbellulata DC., Prodr. 1: 588. 1824.—TYPE: DOMINICAN REPUBLIC: "in Sancto Domingo," Bertero s.n. (holotype: G-DC, microfiche, photo: MICH!).

Banisteria periplocifolia α *subovata* DC., Prodr. 1: 589. 1824.—TYPE: unknown.

Banisteria periplocifolia β *angustifolia* DC., Prodr. 1: 590. 1824.—TYPE: specimen in herb. Balbis (TO).

Banisteria microphylla Hamilton, Prodr. fl. Ind. occ. 40. 1825.—TYPE: specimen in herb. Desvaux, fide Adr. Jussieu, 1843 (P?).

Stigmaphyllon emarginatum f. II. *parvifolium* Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 7. 1899.—TYPE: JAMAICA. Prope Kingston, Oersted s.n. (lectotype, here designated: C!).

Stigmaphyllon periplocifolium f. II. *intermedium* Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 7. 1899.—TYPE: JAMAICA. McNab s.n. (lectotype, here designated: GOET!).

Stigmaphyllon periplocifolium f. III. *microphyllum* Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 7. 1899.—TYPE: HAITI. Bertero 28x (holotype: B, destroyed).

Stigmaphyllon periplocifolium f. IV. *sericans* Nied., Verz. Vorles. Ak. Braunsberg W.-S. 1912–1913: 24. 1912. *Stigmaphyllon lingulatum* var. *sericans* (Nied.) Nied. in Urban, Symb. Antil. 8: 336. 1920.—TYPE: HAITI. Gonaives, Buch 616 (holotype: B, destroyed).

Stigmaphyllon haitiense f. 1. *ovatum* Urban & Nied. in Urban, Symbol. Antil. 7: 243. 1912.—TYPE: HAITI. Christ 1772 (holotype: B, destroyed).

Stigmaphyllon haitiense f. 2. *linearis* Urban & Nied. in Urban, Symbol. Antil. 7: 243. 1912.—TYPE: HAITI. Christ 1771 (holotype: B, destroyed).

Stigmaphyllon rubrinervum Alain, Mem. New York Bot. Gard. 21(2): 122. 1971.—TYPE: Liogier 11863 (holotype: NY!; isotypes: GH! P! US!).

Laminas 1.1–13 cm long, 0.5–10.5 cm wide, extremely variable: linear, lanceolate, oblong, elliptical, ovate, or sometimes suborbicular, apex mucronate-emarginate or sometimes mucronate, base truncate to cordate, sometimes oblique, glabrate to glabrous above and below or sometimes sparsely sericeous below or rarely sericeous below, margin eglandular, basal glands prominent, sessile, each 0.3–1.2 mm in diameter, sometimes pegshaped and up to 0.5 mm high, or gland sometimes absent; petioles 0.2–2 (–3) cm long; stipules triangular to sublinear, eglandular. Flowers (6–) 15–25 (–35) per open to congested pseudoraceme or sometimes an umbel or rarely a corymb, these usually borne solitary, sometimes in dichasia. Peduncles 1.3–25 mm long, pedicels 3–23 mm long, terete, peduncles $\frac{1}{3}$ as long as to equalling the pedicels; bracts 1–2.4 mm long, narrowly triangular, bracteoles 0.6–1.3 mm long, linear to narrowly triangular, eglandular. Limb of lateral petals 7.5–11 mm long and wide, orbicular, limb of posterior petal 6.5–9.5 mm long and wide, broadly ovate to orbicular to oblate, all with the margin erose. Stamens unequal, those opposite the posterior styles the largest, or sometimes stamens opposite the styles subequal, those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers glabrous or sparsely pubescent. Anterior style 2–2.8 mm long, shorter than the posterior two, glabrous; apex 0.5–0.7 mm long including a spur up to 0.4 mm long or blunt, folioles absent. Posterior styles 2.5–3.6 mm long, glabrous, canaliculate-complicate, erect; apex 0.5–1 mm long including a spur up to 0.3 mm long or blunt, folioles absent. Dorsal wing of samara 1.6–2.2 cm long, 0.7–0.9 cm wide, upper margin with a tooth; nut ribbed and commonly bearing spurs and/or crests; embryo ovoid, ca two times as long as wide. Fig. 3.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Jamaica, Hispaniola, Puerto Rico, Virgin Islands, and the Lesser Antilles south to Martinique, not reported from Dominica; on limestone and serpentine outcrops, common in coastal thickets; sea level to 1500 m.

REPRESENTATIVE SPECIMENS. JAMAICA. St. Andrew: Palisadoes, *Yuncker 17293* (F, G, MICH, MO, S); Jack's Hill, *Yuncker 18144* (F, G, MICH, MO, S). St. Catherine: Spanish Town Rd, *Harris 9232* (F, NY, US); Longville Park to Old Harbour Bay, *Harris 11947* (F, MO, NY, S, US). St. James: Montego Bay to Round Hill Bluff, *Harris 10350* (F, NY, US).—HAITI. Massif des Matheux, Thoma-zeau, Morne à Cabrites, *Ekman H930* (F, MICH, S); Massif de la Selle group, Morne des Commissaires, Anses-à-Pitre, *Ekman H6712* (A, G, NY, S, US); Massif du Nord, Vallière, *Ekman H9942* (G, LL, S, US); base of Morne à Cabrites, *Holdridge 1077* (F, GH, MICH, NY); Dept. de l'Artibonite, vic. of Ennery, *Leonard 9713* (GH, S); vic. of Port de Paix, *Leonard & Leonard 12352* (GH, NY, US); vic. of Jean Rabel, E of Bord du Mer, *Leonard & Leonard 13613* (A, GH, US); Tortue Island, vic. of Basse Terre, *Leonard & Leonard 14045* (A, US).—DOMINICAN REPUBLIC. Prov. Azua: E of Azua, *Howard & Howard 8649* (GH, MICH, NY, S); Prov. Barahona: Barahona, *Fuertes 21* (BR, F, G, GH, MO, NY, P, S, U, W); Prov. Monte Christi: near Puerto Libertador, Manzanilla Bay, *Howard & Howard 9667* (GH, NY, S); Prov. Samaná: Los Bañaderos Prietos, *Ekman H15123* (A, NY, S); Prov. Santiago: dist. San José de las Matas, Magua, *Valeur 961* (C, G, LL, MO, NY); Prov. Seibo: vicinity of Higüey, *Howard 9752* (A, MICH, NY); prope Constanza, *von Türckheim 3246* (BR, F, G, GH, M, MO, NY, S, U, US, W).—PUERTO RICO. Culebra Island, *Britton & Wheeler 44* (F, NY); vic. of Coamo Springs, *Britton et al. 5960* (G, NY); Condado, *Britton et al. 6632* (G, NY); Guanica, *Liogier 10785* (GH, NY); prope Salinas de Cabo Rojo, *Sintensis 584* (G, GH, GOET, M, P, S); without locality, *Heller & Heller 474* (F, NY).—ST. THOMAS. *Britton & Shafer 378* (C, F, MO, NY); *Eggers 390* (BR, CAS, G, GOET, M, P, W); *Wylder 40* (BR, F, G).—ST. JOHN: *Britton & Shafer 515* (NY).—TORTOLA. *Britton & Shafer 871* (NY); *D'Arcy 793* (A).—ANEGADA. *Britton & Fishlock 1045* (NY); *D'Arcy 4863* (MO).—VIRGIN GORDA. *Fishlock 68* (NY); *Gillis 5825* (A, MSC).—ST. CROIX. *Hunnewell 20114* (GH); *Ricksecker 154* (F, GH, MO, NY).—ANGUILLA. *Howard & Kellogg 19053, 19057* (MICH).—ST. MARTIN. *Boldingh 2629* (NY, U); *Stoffers 2673* (A, U).—ST. BARTHÉLEMY. *Questel 54* (NY, P), *630* (NY).—ST. EUSTATIUS. *Boldingh 96, 191* (U).—BARBUDA. *Box*



FIG. 3. *Stigmaphyllon emarginatum*. a. Flowering branch ($\times 0.5$). b–j. Leaves ($\times 0.5$); detail of base (h, $\times 2.5$; j, $\times 5$). k. Inflorescence axis with persistent peduncles ($\times 2.5$). l. Section of androecium, anterior stamen on extreme left, posterior stamen on extreme right ($\times 5$). m. Gynoecium ($\times 5$). n. Apical portion of styles, posterior style on right, anterior style on left ($\times 10$). o. Samaras and torus ($\times 1.5$). p. Embryo ($\times 5$). (Based on: a, k, *Valeur* 416; b, *Yuncker* 17293; c, *Liogier* 15180; d, *Liogier* 17597; e, *Howard & Howard* 8649; f, *Liogier* 14820; g, *Liogier* 12442; h, *Yuncker* 18144; i, *Liogier & Liogier* 26900; j, *Leonard & Leonard* 11787; l, *Yntema* 354A; m, n, *Liogier* 12442, anterior style detail, *Yntema* 354A; o, p, *Yntema* 354A, laterally winged samara on left *Leonard* 12352.)

612 (MO).—NEVIS. *Proctor* 19607 (A).—ANTIGUA. *Rose et al.* 3497 (NY).—GUADELOUPE. *Bena* 1944 (P); *Stehlé* 121 (NY).—MARTINIQUE. *Belanger* 553 (P); *Duss* 439 (NY).

Typical plants of this variable species have glabrous or sometimes sparsely sericeous stems and leaves, and bear ca 15–25 flowers in solitary pseudoracemes. Most distinctive are the posterior styles, which are canaliculate-complicate and erect, and efoliolate; the anterior style is also efoliolate but may bear a short spur. All stamens are fertile. The peduncles vary from $\frac{1}{3}$ to equally as long as the pedicels. *Stigmaphyllon emarginatum* is most commonly confused with the often sympatric *S. diversifolium*. In addition to the structure of the styles, *S. diversifolium* differs in having the stamens opposite the lateral sepals sterile and the peduncles much less than $\frac{1}{3}$ as long as the pedicels or absent. See *S. diversifolium* for a more detailed separation.

Like *S. diversifolium*, *S. emarginatum* is conservative in floral characters but bewilderingly variable in leaf shape, sometimes even on the same plant, throughout its range. An astonishing variety is found on Hispaniola alone; seven of the ten leaf shapes illustrated here are based on collections from that island (Fig. 3a, c–g, j; b, h from Jamaica, i from Puerto Rico). The long list of synonyms reflects attempts to subdivide this species on the basis of leaf morphology; however, all the extremes in variation are linked by intermediate forms and are not recognized taxonomically here.

Stigmaphyllon emarginatum is common throughout the West Indies, though absent from Cuba and the Bahamas and not reported from Dominica. The Cuban record, *Ekman* 8607, of Niedenzu (1928) and Liogier (1963) is *S. microphyllum*.

***Stigmaphyllon floribundum* (DC.) C. Anderson, Syst. Bot. 11: 128. 1986.** *Banisteria floribunda* DC., Prodr. 1: 589. 1824.—TYPE: PUERTO RICO. *Bertero* s.n. (holotype: TO, photo: MICH!).

Banisteria tomentosa Desf. ex DC., Prodr. 1: 589. 1824. *Stigmaphyllon tomentosum* (Desf. ex DC.) Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 5. 1899, non *Stigmaphyllon tomentosum* Adr. Juss., 1832.—TYPE: specimen made from plants cultivated at the Botanical Garden in Paris (holotype: G–DC, microfiche: MICH!).

Laminas 3.6–18 cm long, 2.5–15.5 cm wide, elliptical or broadly so, oblong, sometimes lanceolate or suborbicular, apex mucronate or mucronate-emarginate, base truncate to slightly cordate or sometimes acute, glabrous above, sericeous to tomentose below, the indumentum sloughed off in patches and older leaves then glabrate to glabrous, margin eglandular, basal glands prominent, sessile, each 0.5–0.8 mm in diameter; petioles (4–) 8–17.5 cm long; stipules narrowly triangular, eglandular. Flowers (10–) 20–25 (–45) per congested or sometimes interrupted pseudoraceme, less commonly a corymb or sometimes an umbel, these borne in large thyses or sometimes in dichasia, rarely solitary. Peduncles absent to 1.5 (–4) mm long, pedicels (8–) 10–22 mm long, terete; bracts (0.6–) 1.1–1.7 mm long, narrowly triangular, bracteoles (0.2–) 0.7–1.4 mm long, narrowly triangular to linear, eglandular. Limb of anterior-lateral petals (8–) 9–11.5 mm long and wide, limb of posterior-lateral petals (8–) 9–10.5 mm long and wide, limb of posterior petal 6.5–9 mm long and wide, all orbicular or suborbicular, margin erose. Stamens unequal, those opposite the posterior styles the largest, or the one opposite the anterior style the largest, or those opposite

the styles subequal, anthers of those opposite the lateral sepals sterile, or sometimes anthers of stamens opposite the anterior-lateral sepals with one or two reduced locules; fertile anthers pubescent or glabrous. Anterior style 2.1–3.2 mm long, shorter than the posterior two, sometimes the styles subequal in length, glabrous; apex 0.6–0.7 (–1.2) mm long including a spur 0.2–0.3 (–0.6) mm long, linear, 0.1–0.2 mm wide, folioles absent. Posterior styles (2–) 2.5–3.6 mm long, glabrous, lyrate; apex 0.5–0.6 mm long including a spur up to 0.2 mm long or blunt, linear, ca 0.1 mm wide, folioles absent. Dorsal wing of samara 1.8–3.2 cm long, 0.6–1.2 cm wide, upper margin with a tooth; nut smooth or sometimes bearing spurs and/or crests; embryo ovoid, ca two times as long as wide. Fig. 4.

Phenology. Collected in flower and fruit from October through June.

Distribution. Known only from Puerto Rico, Virgin Gorda, and St. John; on limestone and serpentine outcrops, common in coastal thickets, barrens, dunes, pastures, and along roadsides; sea level to 1000 m.

REPRESENTATIVE SPECIMENS. PUERTO RICO. Las Vilyas, NE of Ponce, *Britton & Britton* 7459 (NY); Guayama, *Britton & Britton* 9095 (NY); near Dorado, *Britton & Britton* 9871 (NY); vic. of San Juan, *Britton & Wheeler* 288 (NY); vic. of Vega Baja, *Britton et al.* 5780 (NY, US); Yauco, *Garber* 36 (GH, NY); Caguas, *Goll* 380 (US); near Río Piedras, *Heller & Heller* 972 (NY); 5 mi NE of Mayaguez, *Heller* 4455 (G, GH, MICH, MO, NY, P, US; F is *S. emarginatum*); along rte 687 near Laguna Tortuguero, *Howard & Nevling* 16996 (A, U); Maricao, *Liogier* 10753 (GH, NY); Cayez, *Liogier et al.* 28408, 32547 (UPR); Fajardo, *Martorell & Liogier* 28046 (UPR); Mayaguez, Mt. Las Mesas, *Otero* 546 (A, CAS, F, MO); Mpio Maricao, Maricao Insular Forest, *Proctor* 39192 (JBSD); inter Sabana Grande et Guanica, *Sintensis* 3843 (C, G, GH, M, MSC, MO, NY, P, S, US); Manatí, *Sintensis* 6716 (F, G, NY, W); 13 km N of Cayey, *Underwood & Griggs* 344 (NY, US); near Coamo Springs, *Underwood & Griggs* 458 (NY, US).—ST. JOHN. *Eggers* 3259 (C).—VIRGIN GORDA. *Fishlock* 319 (GH, NY, US); summit and E slope of Virgin Peak, *Smith* 10579 (A, NY, S, US).

Typical plants of *S. floribundum* have strikingly large, golden-sericeous compound inflorescences of congested or interrupted pseudoracemes, each composed of 20–25 (–45) flowers. The leaves are also usually large (to 18 cm long and 15.5 cm wide) and golden-sericeous below; this pubescence is shed in patches, and older leaves are often glabrate to glabrous. *Stigmaphyllon floribundum*, which is known only from Puerto Rico and two of the Virgin Islands, is very similar to *S. diversifolium* of Cuba and the Lesser Antilles. In both species the stamens opposite the lateral sepals bear sterile anthers (sometimes the anthers of those opposite the anterior-lateral sepals have one or rarely two greatly reduced locules), and the peduncles are either absent or very short (less than 4 mm long). The apex of the anterior style of *S. diversifolium* may be expanded and triangular to rhombic or may be linear with a spur 0.6–1.4 mm long; the posterior styles diverge at the base and curve distally and in the longest curl around the opposing stamens. In *S. floribundum*, the apex of the anterior style is always linear with a tiny spur 0.2–0.3 (–0.6) mm long; the posterior styles are erect proximally and curve toward but never twist around the opposing stamens. The inflorescences of *S. diversifolium* are never as elaborate as those of *S. floribundum* nor are its leaves ever as large (up to 14.7 cm long and up to 6.8 cm wide). The samaras of *S. floribundum* are also larger than those of *S. diversifolium*.

Small individuals of *S. floribundum* may be confused with the sympatric *S. emarginatum*, whose styles are also efoliolate. This species differs in its canaliculate-complicate posterior styles and in its stamens, which are all fertile. Its peduncles are $\frac{1}{3}$ to equally as long as the pedicels.

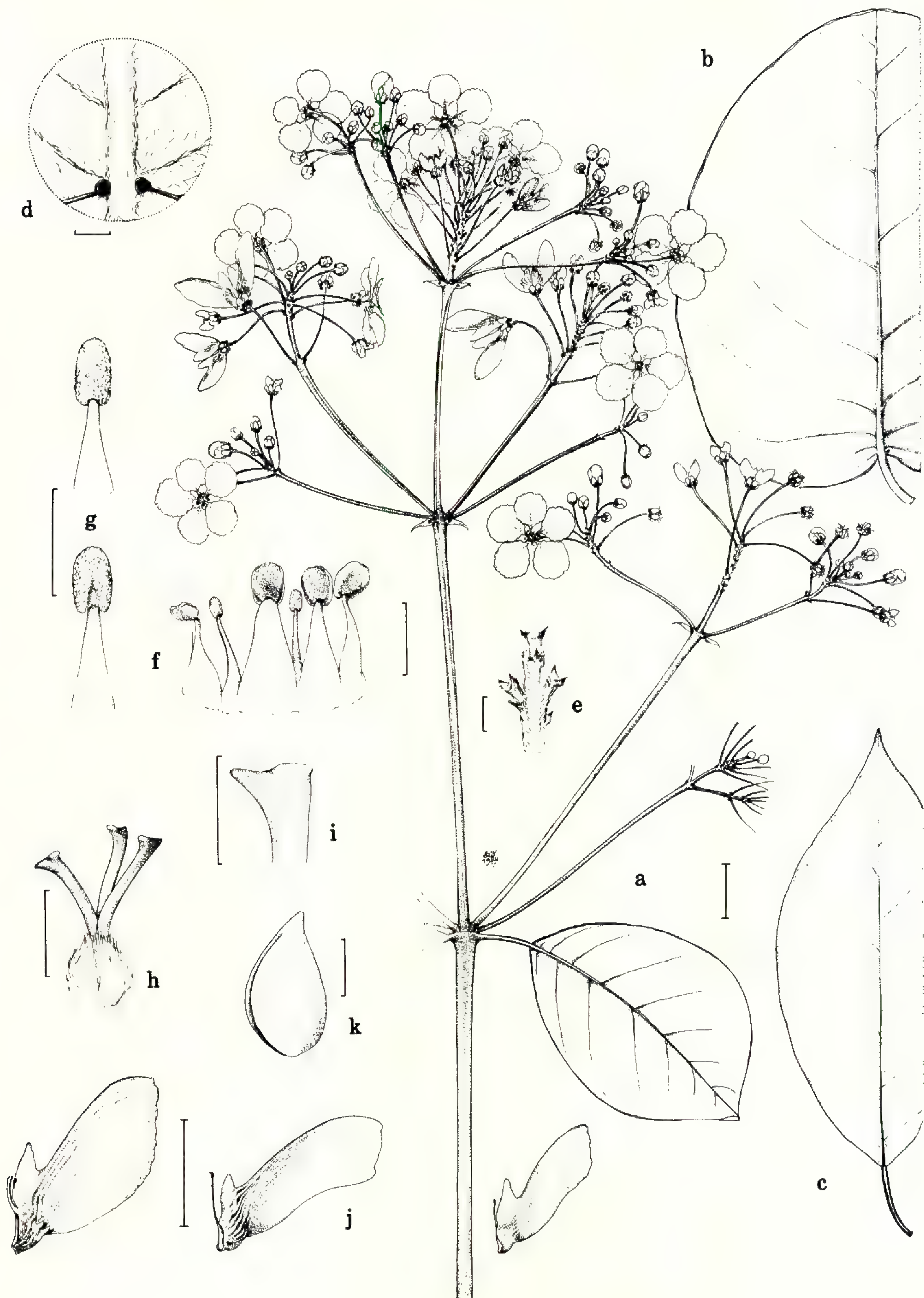


FIG. 4. *Stigmaphyllon floribundum*. a. Habit. b, c. Large leaves. d. Base of leaf and detail of lower surface. e. Section of inflorescence axis with peduncles. f. Section of androecium, posterior stamen on extreme left, anterior stamen on extreme right. g. (above) Abaxial and (below) adaxial view of posterior-lateral stamen. h. Gynoecium. i. Apex of anterior style. j. Samaras. k. Embryo. Scale: for a-c, j, bar = 1.5 cm; for d-f, h, k, bar = 2 mm, for g, i, bar = 1 mm. (Based on: a, e, Colwell 577; b, d, Britton 9871; c, Toro 3; f, g, Liogier 33781; h, i, Tredwell 751; j, Richard s.n., Smith 10579, Sintensis 6716; k, Sintensis 6716.)

Collections of *S. floribundum* are usually identified as *S. tomentosum* (Desf. ex DC.) Nied., an illegitimate name (Anderson 1986).

Stigmaphyllon humboldtianum (DC.) Adr. Juss. in St.-Hil., Fl. Bras. merid. 3: 56. 1832 [1833]. *Banisteria tiliaefolia* H.B.K., Nov. gen. sp. 5: 162. 1821 [1822], non *Banisteria tiliaefolia* Vent., 1808. *Banisteria humboldtiana* DC., Prodr. 1: 588. 1824. *Stigmaphyllon tiliifolium* (H.B.K.) Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 16. 1900. *Stigmaphyllon tiliifolium* var. α . *typicum* Nied., Pflanzenreich IV. 141(2): 497. 1928.—TYPE: COLOMBIA. Bolívar: “. . . inter Carthagenam et Cerro de la Popa,” *Humboldt & Bonpland s.n.* (holotype: P-HBK!).

Banisteria variifolia DC., Prodr. 1: 588. 1824.—TYPE: COLOMBIA. Magdalena: “Ad Sanctam-Martham,” *Bertero s.n.* (holotype: G-DC, photos: F! GH! MICH! NY!).

Banisteria varia Sprengel, Syst. veg. 2: 386. 1825.—TYPE: COLOMBIA. “Ad fl. Magalen [Magdalena],” *Bertero s.n.* (holotype: B, destroyed).

Stigmaphyllon tiliifolium var. γ . *berteroanum* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 17. 1900.—TYPE: COLOMBIA. Magdalena: “Santa Martha,” *Bertero 2647+* (lectotype, here designated: M!).

Laminas 6.2–23 cm long, 4.5–24 cm wide, usually cordate to ovate, sometimes elliptical to suborbicular, or sometimes 3–5-lobed, apex mucronate, base cordate or sometimes truncate or briefly attenuate, glabrate to glabrous above, densely pubescent with T-shaped hairs to densely tomentose below, margin with sessile glands and with scattered filiform glands up to 6 mm long, basal glands prominent, sessile, each 1–2.8 mm in diameter; petioles 1.7–10 cm long; stipules triangular, eglandular. Flowers 15–40 (–50) per umbel or corymb, these borne in dichasia, compound dichasia, or thyrses. Peduncles 3.5–9 mm long, pedicels 4–11 mm long, terete, peduncles and pedicels subequal or equal; bracts 0.5–1.3 mm long, triangular, bracteoles 0.5–1.5 mm long, oblong to triangular, eglandular. Limb of anterior-lateral petals 8–8.6 mm long, 7.5–8 mm wide, limb of posterior-lateral petals ca 7.5 mm long, ca 6.5–7 mm wide, all orbicular, margin denticulate or denticulate-fimbriate, fimbriae up to 0.3 (–0.4) mm long; limb of posterior petal 6–6.5 mm long, 4–4.5 mm wide, elliptical to oblong, margin with fimbriae up to 0.5 mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 2–2.7 mm long, shorter than the posterior two, glabrous; apex 1.2–1.5 mm long, each foliole 1.3–1.6 mm long, 1.4–2 mm wide, square to sometimes subrectangular. Posterior styles 2.7–3 mm long, glabrous, lyrate; folioles 1.3–1.6 mm long, 1.4–2 mm wide, square to sometimes subrectangular. Dorsal wing of samara 3.7–4.5 cm long, 1.2–1.5 cm wide, upper margin with a tooth; nut with a pair of lateral winglets or bearing spurs and/or crests or with only one or two lateral ridges; embryo flattened, ca three times as long as wide. Fig. 5i–o.

Phenology. Collected in flower from September through March, in fruit from November through April.

Distribution. Darién, Panama, and northwestern South America; in dry situations; sea level to 1275 m.



FIG 5. *Stigmaphyllon retusum* and *S. humboldtianum*. a-h, *S. retusum*: a. Flowering branch ($\times 0.5$); detail of lower surface of lamina ($\times 15$). b. Lobed leaf ($\times 0.5$). c. Umbel ($\times 1.5$). d. Posterior petal ($\times 2.5$). e. Androecium ($\times 5$). f. Gynoecium ($\times 5$). g. Samaras ($\times 1$). h. Embryo ($\times 5$). i-o, *S. humboldtianum*: i. Flowering branch ($\times 0.5$); detail of lower surface of lamina ($\times 15$). j. Umbel ($\times 1.5$). k. Posterior petal ($\times 2.5$). l. Section of androecium, posterior stamen on extreme left, anterior stamen on extreme right ($\times 5$). m. Gynoecium and lateral view of anterior style ($\times 5$). n. Samaras ($\times 1$). o. Embryo ($\times 3.5$). (Based on: a, c-f, Fryxell & Anderson 3485; g, Fryxell & Anderson 3522 (Mexico), Sandino 2571 (Nicaragua); h, Pipoly 4542; i, j, Smith 1525; k-m, de Bruijn 1556; n, Romero C. 2045, Fryxell et al. 4400; o, Romero C. 2045.)

REPRESENTATIVE SPECIMENS. PANAMA. Darién: trail between Pinogana and Yavisa, *Allen* 267 (A, F, GH, MO); between Río Jesús and Sabado, *Hammel* 1348 (MO); Río Jaqué valley, 7°27'N, 78°05'W, *Knapp & Mallet* 3203 (MICH); Chepijana dist., Tucute, *Terry & Terry* 1376 (F, GH, MO); Marranganti and vicinity, *Williams* 987 (NY).

Stigmaphyllon humboldtianum, a species of northern Colombia and north-western Venezuela, extends into southern Panama. It is sometimes listed in floras under the illegitimate name *S. tiliifolium*. Reports from Mexico and most of Central America are based on misidentified collections of *S. lindenianum*, which occurs in Darién, Panama, and especially of the variable *S. retusum*, which does not. *Stigmaphyllon humboldtianum* is readily separated from these species by its glabrous anthers; those of *S. lindenianum* and *S. retusum* are pubescent. The embryos of *S. humboldtianum* are unusual in that they are flattened; those of most species, including *S. lindenianum* and *S. retusum*, are ovoid. The leaves of *S. lindenianum* are sericeous below; those of *S. humboldtianum* and *S. retusum* have T-shaped hairs or are tomentose below.

Stigmaphyllon hypargyreum Tr. & Pl., Ann. Sci. Soc. Nat. Bot., sér. 4, 18: 318. 1862.—TYPE: PANAMA. *Duchassaing s.n.* (holotype: P!).

Laminas 7–17.5 cm long, 4.5–12 cm wide, elliptical to ovate or rarely suborbicular, apex acuminate-mucronate, base cordate to truncate or sometimes attenuate, glabrate to glabrous above, densely silvery sericeous below, margin eglandular or with scattered sessile glands, basal glands prominent, sessile, each 1.5–2 mm in diameter; petioles 2.3–7 cm long; stipules narrowly triangular to sublinear, eglandular. Flowers (15–) 20–25 per umbel, these borne in dichasia or small thyrses. Peduncles 2–4 mm long, pedicels 4–7 mm long, terete, peduncles $\frac{1}{2}$ – $\frac{2}{3}$ as long as pedicels; bracts 1.1–2 mm long, triangular, bracteoles 0.9–1.4 mm long, subsquare to parabolic, eglandular. Limb of anterior-lateral petals ca 8–9 mm long and wide, limb of posterior-lateral petals ca 4.5 mm long and wide, all orbicular, margin erose or denticulate or sometimes with fimbriae up to 0.2 (–0.3) mm long; limb of posterior petal ca 4.5 mm long, ca 3.5 mm wide, broadly elliptical, margin erose or denticulate or sometimes with fimbriae up to 0.2 (–0.3) mm long. Stamens unequal, that opposite the anterior style larger than those opposite the posterior styles, those opposite the anterior-lateral sepals usually the longest (sometimes subequal to that opposite the anterior style) and with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3.4–3.7 mm long, longer than the posterior two, glabrous; apex 1–1.2 mm long, each foliole 0.8–1.1 mm long, ca 0.6 mm wide, oblong to triangular. Posterior styles 3–3.5 mm long, glabrous, lyrate; folioles 1–1.4 mm long, 0.8–1 mm wide, oblong to obovate. Dorsal wing of samara 3.5–4.2 cm long, at the nut 0.3–0.4 cm wide and flared distally to 1.1–1.4 cm wide, upper margin without a tooth; nut sometimes with a pair of lateral winglets, more commonly bearing spurs and/or crests; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower from October through July, in fruit from December through April.

Distribution. Canal Zone, San Blas, and Darién, Panama, and Colombia; in moist tropical forest, at forest edge, river margins, in clearings and scrub, and along roadsides; sea level to 350 m.

REPRESENTATIVE SPECIMENS. PANAMA. Canal Zone: between Farfan Beach and Palo Seco, *Hunter & Allen 440* (F, G, MO, U); ca 1 mi SW of Cocoli in the Rodman Naval Ammunition Depot, *Wilbur et al. 12871* (F, NY, US); rd from Cocoli to Contractor's Hill, *Tyson & Lazor 6164* (MO); Pipeline Road, 3–5 mi from Gamboa, *Gentry 2415* (F, MO, NY); Barro Colorado Island, *Croat 7226* (F, MO, NY), *Wilson 156* (F), *Woodworth & Vestal 621* (A, F, MO). Darién: Ensenada del Guayabo, 18 km SE of Jaqué, *Garwood et al. 158* (MICH, MO). San Blas: Ailigandí, *Hammel & D'Arcy 5029* (MICH).

Stigmaphyllon hypargyreum is named for the silvery sericeous pubescence on the lower leaf surfaces, which is so dense that the epidermis is obscured. It is one of the two species in our area in which the anterior style and its opposing stamen are larger than the posterior styles and their opposing stamens. The other species is *S. puberum*, whose leaves are sericeous or very sparsely so below; the epidermis is always visible. The two also differ in their samaras. Those of *S. hypargyreum* are of the type most common in the genus. The dorsal wing is flared and widest beyond the midpoint, but it differs from most other species in that it is greatly narrowed at the point of insertion. The nut commonly bears spurs and/or crests or sometimes lateral winglets. In *S. puberum* the dorsal wing encircles the nut and tapers distally; the nut is smooth or at most ribbed.

The only other species in our area whose leaves may be so densely pubescent below is *S. pseudopuberum* of Chiapas, Mexico, and adjacent Guatemala. It has small flowers with subequal, efoliolate styles and subequal stamens.

Stigmaphyllon laciniatum (Ekman ex Nied.) C. Anderson, comb. nov. *Stigmaphyllon angulosum* f. *laciniatum* Ekman ex Nied. in Urban, Arkiv Bot. 22A(17): 19. 1929.—TYPE: HAITI. Île de la Gonâve, *Ekman 8820* (holotype: B, destroyed; isotypes: NY! S! US!).

Laminas 3–12 cm long, 4–11 cm wide in outline, lacinate, apex of each division mucronate, base cordate, sparsely sericeous to glabrate above, sericeous to sparsely so to glabrate below, margin with sessile glands and filiform glands up to 2.5 mm long, basal glands prominent, sessile, each 1–1.7 mm in diameter; petioles 1–5 cm long; stipules triangular, eglandular. Flowers 13–22 per corymb or open to congested, sometimes interrupted pseudoraceme, these borne in dichasia or compound dichasia or sometimes solitary. Peduncles 2.3–7.5 mm long, pedicels 4–7 mm long, terete, peduncles usually shorter than but sometimes subequal to the pedicels; bracts 1–1.5 mm long, triangular, bracteoles 1.1–1.7 mm long, broadly triangular, eglandular. Limb of anterior-lateral petals 11–12 mm long and wide, limb of posterior-lateral petals ca 10 mm long and wide, limb of posterior petal ca 9 mm long and wide, all orbicular, margin denticulate or entire near the claw, distally with fimbriae up to 0.4 mm long. Stamens unequal, those opposite the posterior styles the largest, anthers of those opposite the anterior-lateral sepals sterile, those opposite the posterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3–3.2 mm long, shorter than the posterior two, glabrous; apex ca 0.7 mm long, each foliole 1.3–1.4 mm long, 1.2–1.3 mm wide, parabolic. Posterior styles 3.6–3.7 mm long, glabrous, lyrate; folioles 1.7–2 mm long, ca 1.7 mm wide, subsquare. Dorsal wing of samara 1.5–1.8 cm long, 0.5–0.7 cm wide, upper margin with a tooth; nut with a pair of lateral winglets or sometimes only with a narrow ridge on each side; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit in July and August.

Distribution. Endemic to Île de la Gonâve, west of Haiti.

ADDITIONAL SPECIMENS EXAMINED. HAITI. Île de la Gonâve: *Ekman* 8670 (NY—fragment, S); *Eyerdam* 63 (F, GH, US), 219 (A, F, GH, MO, NY, US).

Stigmaphyllon laciniatum was first described as a form of *S. angulosum* of Hispaniola. While it is probably most closely related to that species, it differs from it consistently and is here accorded specific status. It is the only species in the genus to have lacinate leaves. *Stigmaphyllon angulosum* has sinuate-lobate leaves, also unique in the genus. The two species are similar in their flowers though those of *S. laciniatum* are somewhat smaller. In *S. laciniatum* the stamens opposite the anterior-lateral sepals bear sterile anthers; in *S. angulosum* all anthers are fertile. The two also differ in the size of their samaras. The dorsal wing is 1.5–1.8 cm long in *S. laciniatum* and 2.8–4.5 cm long in *S. angulosum*.

Stigmaphyllon lindenianum Adr. Juss., Arch. Mus. Hist. Nat. Paris 3: 362. 1843.

Stigmaphyllon lindenianum subsp. *a. typicum* Nied., Pflanzenreich IV. 141(2): 499. 1928. *Stigmaphyllon lindenianum* var. *β. jussieuianum* Nied., Pflanzenreich IV. 141(2): 499. 1928, nom. superfl.—TYPE: MEXICO. Tabasco: Teapa, *Linden s.n.* (holotype: P!; isotype?: G!).

Stigmaphyllon tiliifolium var. *δ. sericans* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 17. 1900. *Stigmaphyllon sericans* (Nied.) Small, N. Amer. fl. 25(2): 144. 1910.—TYPE: HONDURAS. Santa Bárbara: Pedro Sula, 800 ft, *Thieme* 5164 (lectotype, here designated: US!; isoelectotypes: GH! NY!).

Stigmaphyllon lindenianum var. *α. yucatanum* Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 18. 1900.—TYPE: MEXICO. Yucatán, *Gaumer* 408 (holotype: B, destroyed; isotypes: A! BR! C! CAS! F! MICH! MO! NY! US! W!).

Stigmaphyllon tiliifolium var. *δ. sericans* f. II. *grandifolia* Nied., Pflanzenreich IV. 141(2): 498. 1928.—COSTA RICA. Cartago: Tuis, Turrialba, 650 m, *Tonduz* 11454 (lectotype, here designated: F!; isoelectotypes: BR! M! MICH! US!).

Laminas (4.5–) 5–18.5 cm long, 4–15.5 cm wide, triangular to ovate to cordate, sometimes 3–5-lobed or elliptical, apex mucronate to caudate, base cordate to subtruncate, glabrate to glabrous above, sericeous to sparsely so below, margin with scattered sessile glands and/or with scattered filiform glands up to 2.5 mm long, basal glands prominent, sessile, each 1.2–3.2 mm in diameter; petioles (1.1–) 1.6–8.5 (–10) cm long; stipules triangular, eglandular. Flowers (9–) 12–35 per umbel or corymb, these borne in dichasia, compound dichasia, or small thyrses. Peduncles 2.7–8.5 mm long, pedicels (3.5–) 3.8–9.5 (–10.5) mm long, terete, peduncles usually longer than but sometimes shorter than or equalling the pedicels; bracts 0.8–15 mm long, narrowly to broadly triangular, bracteoles 0.7–1.4 mm long, oblong or sometimes broadly triangular, eglandular. Limb of anterior-lateral petals 7–9.3 (–10) mm long, 6–8.5 (–9) mm wide, limb of posterior-lateral petals 5.5–8.5 mm long, 5–6.5 mm wide, all obovate to orbicular, margin erose, denticulate, or denticulate-fimbriate, fimbriae up to 0.2 (–0.3) mm long; limb of posterior petal 5.8–7 (–7.5) mm long, 4–5 mm wide, elliptical to obovate, margin erose, denticulate-fimbriate, or with fimbriae up to 0.2 (–0.3) mm long. Stamens unequal, those

opposite the posterior styles the stoutest, equally long or slightly longer than those opposite the lateral sepals, those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers pubescent, those with reduced locules glabrous. Anterior style (1.8–) 2–3 mm long, shorter than the posterior two, glabrous; apex 0.8–1.5 mm long, each foliole 0.5–1 mm long, 0.7–1.1 mm wide, triangular to parabolic or sometimes subsquare to narrowly trapezoidal to subrectangular, rarely the folioles reduced and the apex only expanded, rhombic, 0.4–0.5 mm wide. Posterior styles 2.3–3.5 mm long, glabrous, lyrate; folioles 0.9–1.3 (–1.7) mm long, 1–1.5 (–1.7) mm wide, subsquare to subrectangular. Dorsal wing of samara 2–3.5 cm long, 0.6–1.4 cm wide, upper margin usually with a tooth; nut smooth or with 2–3 winglets on each side or bearing spurs and/or crests; embryo ovoid, ca two times as long as wide. Fig. 6a–g.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Atlantic lowlands from southern Veracruz, Mexico, to Panama, in Costa Rica also reported from the Golfo Dulce area, in Panama also in the Pacific lowlands; in tropical deciduous forest, secondary evergreen forest, mangrove swamps, and at roadsides; sea level to 1200 m.

REPRESENTATIVE SPECIMENS. MEXICO. Chiapas: Mpio Ocozocoautla de Espinosa, 45 km N of Ocozocoautla, *Breedlove* 20724 (CAS, ENCB, MICH, MO); Mpio Solosuchiapa, below Ixhuatán along road to Pichucalco, *Breedlove* 34871 (CAS, ENCB, MEXU, MICH); Mpio Las Margaritas, confluence of Río Ixcán with Río Lacantum (Río Jataté), *Breedlove* 34226 (CAS, MICH, NY). Oaxaca: Mpio Sta María Chimalapa, dist. Juchitán, 4 km al NO del Ejido La Esmeralda, *Delgado S. et al.* 952 (CAS, CHAPA, ENCB, F, MEXU, NY). Quintana Roo: NW del entronque Chetumal–F. Carillo Puerto, *Téllez* 2013 (MEXU, MO); 21 km al SE de Chunhuhub, *Téllez* 2180 (MEXU, MO). Tabasco: Mpio Huimanguillo, KM 35 de la desviación de Huimanguillo hacia Fco. Rueda, *Cowan* 2679 (CAS, CHAPA, ENCB, TEX); Mercedes, Balancán, *Matuda* 3022 (A, F, MEXU, MICH, NY). Veracruz: La Palma, Catemaco, *Martínez Calderón* 2201 (A, CAS, MEXU); Hidalgotitlán, *Vázquez* 390 (F, MEXU, MO). Yucatán: SE Kancabconot, *Gaumer* 23900 (C, F, G, GH, MO, NY, US); Mpio Tunkas, Quintana Roo, *Vara & Arias* 320 (CAS, CHAPA, ENCB, F, MO).—GUATEMALA. Alta Verapaz: along Río Sebol, downstream from Carizal, *Steyermark* 45796 (A, F, LL); Cobán, *von Türckheim II*–2359 (F, US). Izabal: vic. of Quiriguá, *Standley* 24055 (GH, NY, US). Petén: Poptún, carretera para San Luis, *Tún Ortiz* 2137 (F, MICH, US).—BELIZE. Orange Walk: Roaring Creek, *Dwyer & Liesner* 12259 (MICH, MO, NY). Stann Creek: Middlesex, *Schipp* 468 (A, F, G, GH, MICH, MO, NY, S).—HONDURAS. Atlántida: along Tela River, between Peñas Gordas and Tela, *Molina R. & Molina* 25678 (F, MO, NY, US). Copán: vic. of Copán ruins, *Molina R. & Molina* 24605 (F, MO, NY). Cortés: a orillas del Río Lindo, *Molina R.* 11828 (F, NY, US, UTD). Islas de la Bahía: Roatán Island, *Molina R.* 20698 (F, NY, US). Santa Bárbara: al N de Santa Bárbara, región La Cuesta, *Molina R.* 3770 (F).—NICARAGUA. Río San Juan: between San Juan del Norte and Delta de San Juan, *Bunting & Licht* 837 (DUKE, F, NY, US); Caño El Roble, *Moreno* 23367 (MICH); Archipiélago de Solentiname, N Isla La Venada, *Sandino* 3603 (MICH). Zelaya: Monkey Point, *Moreno & Sandino* 11995 (MICH), 12031 (MO); Caño Montecristo, *Moreno* 15191 (MO); Montecristo, N de Barra Punta Gorda, *Sandino* 2230 (MO).—COSTA RICA. Alajuela: ca 3 km NNE of Bijagua along new rd to Upala, *Burger & Baker* 9877 (F, NY). Heredia: Finca La Selva, OTS field station, *Hammel* 8398, 8461, 9017, 10016, 10661, 11640 (DUKE). Limón: near Río Catarata, 9°37'N, 82°49'W, *Burger et al.* 10415 (CAS, F). Puntarenas: ca 5 km W of Rincón de Osa, Osa peninsula, *Burger & Gentry* 8879 (AAU, DUKE, F, MO, U).—PANAMA. Bocas del Toro: Water Valley, vic. of Chiriquí Lagoon, *von Wedel* 1525, 2754 (GH, MO). Canal Zone: Barro Colorado Island, *Croat* 7021 (F, MO, NY), *Wetmore & Abbe* 220 (F, GH, MO); 4 km NW of Gamboa, *Nee* 7582 (CAS, MO, TEX, U); NW shore of Gatun Lake, ca 4 mi S of Río Chares, *Lewis et al.* 1817 (MEXU, MO). Chiriquí: Burica Peninsula, 2 km S of Puerto Armuelles, *Busey* 475 (F, MO, NY); Paso Canoas to Carras Gordas, 10.5 km N of Paso Lanoas, *Busey* 615 (F, MO, NY). Colón: rd from Colón to Porto Belo, 24.6 km E of transisthmian hwy, *Folsom* 3730 (MO, MICH); at Quebrada Santa Marta on coast rd 4½ km SW of Pina, *Nee* 11717 (F, MO, US); Santa Rita Ridge, ca 15 mi from hwy at Sabanita, *Wilbur & Luteyn* 11845 (F, NY, US). Darién: Río Chucunaque, between Río Membrillo and Río Subcuti, *Duke* 8609 (MO); Río Ucungati, *Bristan* 1172 (MO). Panamá: Río Majé, above first water-



FIG. 6. *Stigmaphyllon lindenianum*, *S. panamense*, and *S. tonduzii*. a-g, *S. lindenianum*: a. Flowering branch ($\times 0.5$). b. Lobed leaf ($\times 0.5$), detail of lower surface of lamina ($\times 10$). c. Posterior petal ($\times 2.5$). d. Section of androecium, posterior stamen on extreme left, anterior stamen on extreme right ($\times 5$). e. Gynoecium ($\times 5$). f. Samaras ($\times 1$). g. Embryos ($\times 5$). h-l, *S. panamense*: h. Flowering branch ($\times 0.5$), detail of lower surface of lamina ($\times 10$). i. Posterior petal ($\times 2.5$). j. Gynoecium ($\times 5$). k. Androecium ($\times 5$). l. Samara ($\times 1$). m-o, *S. tonduzii*: m. Gynoecium ($\times 5$). n. Samara ($\times 1$). o. Embryo ($\times 5$). (Based on: a, e, MacDougall s.n.; b, c, d, Reznicek M179; f, Cowan 2679, Burger 10415; g, Cowan 2024, 3189; h-k, Johnston 1301; l, Duchassaing s.n.; m-o, Meerow et al. 1003.)

fall, *Croat 34435* (MO); along headwaters of Río Corso (off Río Pacora), *Duke 11937* (MO). San Blas: El Llano-Cartí rd, 9°19'N, 78°55'W, *de Nevers & Pérez 3990* (MICH); Dubaganalla, *Duke 10199* (MO).

Stigmaphyllon lindenianum, one of the most widely distributed species in our area, is common throughout the Atlantic lowlands of southern Mexico and Central America and has also been recorded from the Osa Peninsula of Costa Rica and the Pacific side of Panama. Its relatively small flowers with pubescent anthers and foliolate styles are borne in many-flowered compound inflorescences. The leaves vary from triangular to cordate or sometimes 3–5-lobed. This species is commonly confused with the variable *S. retusum* and also with *S. humboldtianum*. They are most readily separated by their leaves. Those of *S. lindenianum* are sericeous below, i.e., the hairs are straight and tightly appressed, while those of *S. retusum* and *S. humboldtianum* have T-shaped hairs below or are tomentose. Also, the anthers of *S. humboldtianum* are glabrous. The difference in vesture of the lower leaf surface of *S. lindenianum* and *S. retusum* was first pointed out by Morton (1936); however, he applied the name *S. humboldtianum* to *S. retusum* and also preferred to recognize all three taxa as *S. lindenianum*.

In *S. lindenianum* all styles are normally foliolate, but in a few collections from Chiapas (*Laughlin 2905*, DS), Veracruz (*Dorantes 2979*, MEXU, MICH, MO), and Yucatán (*Gaumer 408*, A, BR, C, CAS, F, MICH, MO, NY, US, W) the anterior style bears reduced folioles or lacks folioles and its apex is merely laterally expanded; the degree of reduction may vary even within the same inflorescence. Niedenzu recognized these unusual plants as var. *yucatanum*, based on *Gaumer 408*. Such occasional reduction and loss of the folioles is also known in other species and does not merit taxonomic recognition.

Stigmaphyllon microphyllum Griseb., Pl. Wright. 168. 1860.—TYPE: CUBA. Oriente: Guantánamo, *Wright 93* (holotype: GOET!; isotypes: BR! G! GH! MO! S! US!).

Laminas 0.8–3.7 cm long, 0.4–1.4 cm wide, elliptical to oblong or sometimes obovate, apex mucronate-emarginate, sometimes obtuse, base attenuate or truncate to sometimes subcordate, sparsely sericeous to glabrate to glabrous above, sericeous to sparsely so below, margin eglandular, basal glands stipitate, each 0.2–0.3 mm in diameter, 0.2–0.6 mm long; petioles (0.1–) 0.2–0.4 cm long; stipules narrowly triangular to sublinear, eglandular. Flowers 4 per solitary umbel. Peduncles 3.5–16 mm long, pedicels (0.7–) 0.9–24.5 mm long, terete, peduncles $\frac{1}{3}$ as long as to equalling the pedicels; bracts 0.9–14 mm long, triangular to broadly so, bracteoles 0.7–13 mm long, broadly to narrowly triangular, eglandular. Limb of anterior-lateral petals 8.7–9.3 mm long and wide, limb of posterior-lateral petals ca 8.5–9 mm long and wide, limb of posterior petal 6.5–7.5 mm long and wide, all orbicular, margin erose. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced; anthers pubescent, sometimes sparsely so. Anterior style 2.3–2.8 mm long, shorter than the posterior two, glabrous; apex 0.6–0.8 mm long, each foliole 0.4–0.7 mm long, 0.4–0.5 mm wide, obovate or oblong or parabolic, or rarely the apex only laterally expanded, rhombic, ca 0.5 mm wide. Posterior styles 2.9–3.8 mm long, glabrous, canaliculate-complicate and erect; folioles 0.6–0.7 mm long, 0.4–0.5 mm wide, semielliptical or parabolic or obo-

vate. Dorsal wing of samara 1.6–1.7 cm long, 0.6–0.7 cm wide, upper margin with a tooth; nut commonly bearing spurs and/or crests or smooth; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower in February, March, October, and December, in fruit in May and December.

Distribution. Endemic to Cuba.

ADDITIONAL SPECIMENS EXAMINED. CUBA. Oriente: Novaliches, Guantánamo, *Alain* 3502 (GH); Guantánamo Bay, *Britton* 2252 (NY); Ensenada de Mora, *Britton et al.* 12947 (NY), *Britton et al.* 13028 (F, MO, NY, US); Novaliches, Guantánamo, *Hioram* 2402 (GH, NY); Estación Naval de Caimanera, *Hioram & Ramsden* 2339 (NY); vic. of Manzanillo, *Shafer* 12348 (NY). Camagüey: Santa Cruz del Sur, *Ekman* 8607 (G, NY, S); between Tarafa and Pastilillo, *Ekman* 15463 (S). Havana: Batabanó, La Mora, *Ekman* 12625 (S).

Stigmaphyllon microphyllum is named for its small leaves, which are up to 3.7 cm long and 1.4 cm wide. The basal leaf glands are usually peg- or nail-like, as in *S. sagraeanum*. It is the only species in our area in which the inflorescence is always a solitary, 4-flowered umbel. The posterior styles resemble those of *S. emarginatum* in that they are canaliculate-complicate but differ by bearing folioles. The anterior style is also foliolate though in one collection, *Britton et al.* 13028, each foliole is reduced to a narrow lip.

Stigmaphyllon microphyllum is superficially similar to small-leaved individuals of *S. emarginatum*, which does not occur in Cuba, and has been confused with it (see that species).

Stigmaphyllon ovatum (Cav.) Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 31. 1900. *Banisteria ovata* Cav., Diss. 9: 429. 1790. *Brachypteris borealis* Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 291. 1840, nom. superfl. *Brachypteris ovata* (Cav.) Small, N. Amer. fl. 25(2): 138. 1910.—TYPE. DOMINICAN REPUBLIC. *Surian* 828 (lectotype, here designated: P–JU!).

Banisteria maritima Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792.—FRENCH GUIANA. *LeBlond* 45 (holotype: G!).

Banisteria picta H.B.K., Nov. gen. sp. 5: 160. 1821 [1822].—TYPE: COLOMBIA. “Crescit locis humidis fluminis Sinu, inter Carthagenam et Isthmum Panamensis,” *Humboldt & Bonpland s.n.* (holotype: P–HBK!).

Banisteria brachyptera DC., Prodr. 1: 591. 1824.—TYPE: FRENCH GUIANA. Cayenne, *Perrotet s.n.* (holotype: G–DC, microfiche: MICH!).

Banisteria calcitrapa Hamilton, Prodr. pl. Ind. occ. 40. 1825.—TYPE: *Desvaux s.n.* (holotype: P!).

Stigmaphyllon heringerianum de Paula & Alves, Rodriguésia 46: 165. 1978.—TYPE: BRAZIL. Maranhão: Rosário, cachoeira de Miranda, estuário do rio Itapecuru, 12 Jan 1976, *de Paula* 741 (holotype: UB!).

Laminas 4–12 cm long, 1.5–5.5 cm wide, narrowly elliptical to lanceolate, apex acute, obtuse, or sometimes apiculate, base attenuate or truncate, glabrate to glabrous above, sparsely sericeous below, margin eglandular, basal glands flush, each 0.5–1 mm in diameter; petioles 0.4–1.8 cm long; stipules triangular, eglandular. Flowers (3–) 4 (–6) per umbel, these solitary or borne in dichasia or sometimes in small thyrses. Peduncles 0.2–2.5 mm long, pedicels 15–30 mm long, terete, peduncles much shorter than the pedicels; bracts 1–2.3 (–5.3) mm long, ovate or elliptical, bracteoles 0.8–1.6 mm long, ovate to elliptical or triangular, eglandular. Limb of anterior-lateral petals 11–12 mm long and wide, limb of

posterior-lateral petals 9–12 mm long and wide, limb of posterior petal ca 8.5–10.5 (–11) mm long and wide, all orbicular or broadly obovate, margin erose. Stamens equal in shape, those opposite the anterior-lateral sepals usually the longest, sometimes those opposite the posterior-lateral sepals equally long; anthers equal or subequal, glabrous. Anterior style 2.5–3.7 mm long, equal or subequal to the posterior two, glabrous; apex 1–1.7 mm long, linear, 0.2–0.3 mm wide, folioles absent. Posterior styles 2.6–3.7 mm long, glabrous, erect; apex 1–1.2 mm long, usually 0.1–0.3 mm shorter than apex of anterior style, linear, 0.2–0.3 mm wide, folioles absent. Dorsal wing of samara reduced to an apical crest 4–9 mm high, 5.5–7.5 mm wide; nut bearing 4–6 ridges or winglets (up to 2 mm high, 7 mm wide); embryo circular to horseshoe-shaped.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Atlantic coast from southern Veracruz, Mexico, to northern Brazil, in the West Indies reported from Cuba, Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Martinique, St. Lucia, and Barbados; along seashores and beaches, in mangrove swamps and salt marshes; sea level to 50 m.

REPRESENTATIVE SPECIMENS. CUBA. Oriente: Baracoa, *Ekman 4106* (G, S), *Shafer 3912* (F, NY, US), *Wright 2157* (GH, GOET, MO).—JAMAICA. Portland: *Hunnewell 15299* (GH). St. Mary: Annotto Bay, *Proctor 23755* (LL, NY). St. Thomas: Morant Point, *Webster & Wilson 5229* (G, MICH, S).—HAITI. Dept. du Nord, Bayenne, *Ekman H2668* (A, F, G, LL, NY, S, US); vic. of St. Louis du Nord, *Leonard & Leonard 14099* (A, NY, US); Bayeux, near Port Margot, *Nash & Taylor 1016* (NY).—DOMINICAN REPUBLIC. Samaná peninsula, vic. of Sánchez, *Abbott 516* (GH, US); Prov. Puerto Plata, Puerto Plata, *Ekman 14357* (S, US); Prov. Barahona, *Fuertes 313* (A, F, G, GH, MO, NY, P, S, US, W).—PUERTO RICO. Naguabo prope Río Blanco, *Eggers 407* (BR, G, GH, GOET, M, P, W); mouth of Río Santiago, *Liogier & Liogier 28999* (NY, UPR); Vieques Island, *Woodbury V-14* (UPR).—BARBADOS. *McIntosh 65* (P); *Bovell & Treeman 210* (NY).—GUADELOUPE. *Questel 453, 576, 4993* (US); *Stehlé et al. 5515* (US).—MARTINIQUE. *Sieber 125* (BR, GOET, M, MO, NY, W); *Duss 1414* (F, GH, MO, NY, US).—ST. LUCIA. *Proctor 18024* (A); *Sturrock 270* (A).—MEXICO. Tabasco: Frontera, *Rzedowski 30035* (MEXU, MICH, MO, P). Veracruz: antes de puente de Alvarado, *Calzada 435* (CAS, GH, MEXU).—GUATEMALA. Izabal: Puerto Barrios, *Deam 384* (GH, MICH, NY, US).—BELIZE. Belize: Belize, *Kellerman 5737* (LL, US), *Lundell 4087, 4089* (MICH).—NICARAGUA. Río San Juan: San Juan del Norte (Greytown), *Stevens 20824* (MO). Zelaya: Bahía de Bluefields, *Molina R. 2060* (F); La Barra de Punta Gorda, *Moreno 13196, 13201* (MO); Río Kuawantla, 3 km W of Puerto Isabel, *Neill 4576* (MICH); El Bluff, N de El Muelle, *Sandino 2227* (MICH).—PANAMA. Colón: Chagres, *Fendler 49* (GH, MO, US); Miguel de la Borda, *Croat 10073* (F, MO); trail above Río Indios, *Sullivan 122* (MO). San Blas: vicinity of Cangandi, 9°24'N, 79°24'W, *de Nevers et al. 6442* (MO).

Stigmaphyllon ovatum is an atypical, easily recognized species. The large flowers, borne in groups of (3–) 4 (–6) per umbel, differ from most species in their subequal stamens and subequal, efoliolate but hooked styles. The peduncles are always much shorter than the pedicels. The leaves consist of short petioles, less than 2 cm long, and narrowly elliptical to lanceolate laminas; the basal glands are flush rather than prominent as in all other species in our area. Most unusual is the samara. The dorsal wing is reduced to an apical crest 4–9 mm high. The large (8–11 mm in diameter), usually ribbed nut contains a circular to horseshoe-shaped embryo.

Stigmaphyllon panamense C. Anderson, sp. nov.—TYPE: PANAMA. San José Island, Las Perlas Archipelago, ca 55 mi SSE of Balboa, rd to Third Beach, *Johnston 1301* (holotype: GH!; isotype: MO!).

Liana. Laminae 8.2–13 cm longae, 5.5–10.5 cm latae, ovatae vel ellipticae, supra glabrae, subtus pilos T-formes brevissime stipitatos ferentes, margine eglan-

dulosae vel glandulosae. Inflorescentia dichasialis vel thyrsiformis constata ex umbellis, floribus in quaque umbella 13–20. Pedunculi 2.5–7 mm longi; pedicelli 5.5–11 mm longi. Bracteae 1–1.7 mm longae, triangulares; bracteolae 0.7–1.1 mm longae, ovatae vel late ovatae, eglandulosae. Petala lateralia orbicularia, marginibus erosis vel eroso-denticulatis; petalum posticum ellipticum vel late obovatum, margine fimbriata vel denticulato-fimbriata. Stamina heteromorpha, omnia fertilia vel antherae petalis postico-lateralibus oppositae raro steriles; antherae glabrae. Stylus anticus 3–3.2 mm longus, apice 1.7–2.1 mm longo, utroque foliolo 1.4–2.1 mm longo latoque, subquadrato; styli postici 3.9–4.5 mm longi, lyrati, foliolo 1.9–2.8 mm longo latoque, quadrato vel subrectangulari.

Laminas 8.2–13 cm long, 5.5–10.5 cm wide, ovate or elliptical, apex acuminate or acuminate-mucronate, base slightly cordate to truncate, glabrous above, sericeous or with short-stalked (0.05–0.1 mm long) T-shaped hairs below but these sloughed off in patches and old laminas glabrate or glabrous below, margin eglandular or with scattered sessile glands, basal glands prominent, sessile, each 1–1.8 mm in diameter; petioles 2.4–5 cm long; stipules broadly triangular or ovate, eglandular. Flowers 13–20 per umbel, these borne in dichasia or small thyrses. Peduncles 2.5–7 mm long, pedicels 5.5–11 mm long, terete, peduncles ($\frac{1}{3}$ –) $\frac{1}{2}$ (– $\frac{4}{5}$) as long as pedicels; bracts 1–1.7 mm long, triangular, bracteoles 0.7–1.1 mm long, ovate or broadly so, eglandular. Limb of anterior-lateral petals 12–15 mm long and wide, limb of posterior-lateral petals 10–11.5 mm long and wide, all orbicular, margin erose or erose-denticulate; limb of posterior petal 9–11 mm long, ca 7.5 mm wide, elliptical to broadly obovate, margin fimbriate or denticulate-fimbriate, fimbriae (0.1–) 0.2–0.4 (–0.7) mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced, sometimes those opposite the posterior-lateral sepals with only one locule or rarely sterile; anthers glabrous. Anterior style 3–3.2 mm long, shorter than the posterior two, glabrous; apex 1.7–2.1 mm long, each foliole 1.4–2.1 mm long and wide, subsquare. Posterior styles 3.9–4.5 mm long, glabrous, lyrate; folioles 1.9–2.8 mm long and wide, square to subrectangular. Dorsal wing of samara ca 3.7 cm long, ca 1.3 cm wide, upper margin with a tooth; nut with a pair of lateral winglets; mature seed not seen. Fig. 6h–l.

Phenology. Collected in flower from December through February and in April; date unknown of only fruiting collection seen.

Distribution. Central Panama and islands in the Gulf of Panama; in thickets and at forest edge; sea level to 50 m.

ADDITIONAL SPECIMENS EXAMINED. PANAMA. Canal Zone: Farfan Beach, *Dwyer 4002* (MO); near Madden Dam, *Lewis et al. 5299* (MO). Colón: N side of Madden Dam, *Knapp 2729* (MICH). Darién: Isla Saboga, *Duke 10341, 10365* (MO); Isla Casaya, *Duke 10382* (MO). Panamá: Isla Chitré, *Knapp 3221* (MICH); Isla Chapera, *Knapp 3305* (MO). Without locality: *Duchassaing s.n.* (GOET).

Stigmaphyllon panamense has large flowers borne on pedicels that are ($\frac{1}{3}$ –) $\frac{1}{2}$ (– $\frac{4}{5}$) as long as the peduncles. The anthers of the stamens opposite the posterior-lateral petals bear only one reduced locule or rarely are sterile; all anthers are glabrous. The styles all have large folioles; those of the anterior styles are 1.4–2.1 mm long and wide, and those of the posterior styles are 1.9–2.8 mm long and wide. The lower leaf surfaces are sericeous or bear short-stalked T-shaped hairs; the pubescence is sloughed off in patches, and old leaves may be glabrate below.

This species was reported by Johnston (1949) and by Cuatrecasas and Croat (1980) as *S. lindenianum*. *Stigmaphyllon lindenianum* differs in its smaller flowers on pedicels that usually are shorter than the peduncles. All anthers bear two locules and are pubescent. The folioles are smaller, up to 1 mm long and 1.1 mm wide in the anterior style, and up to 1.3 (–1.7) mm long and 1.5 (–1.7) mm wide in the posterior ones. The leaves are sericeous below with the hairs evenly distributed or sparsely so but are never glabrous.

Stigmaphyllon pseudopuberum Nied., Verz. Vorles. Ak. Braunsberg W.-S. 1912–1913: 28. 1913.—TYPE: GUATEMALA. Alta Verapaz: Coban, Nov 1902, *von Türckheim* 8385 (lectotype, here designated: US!; isolectotypes: A! F! GH! M! NY! US!).

Laminas 6–15 cm long, 3.5–12 cm wide, ovate to elliptical or broadly so or sometimes lanceolate, apex acuminate-mucronate, base attenuate to truncate or sometimes slightly cordate, glabrous above, sericeous to densely so below, margin with sessile glands, basal glands prominent to stoutly stalked (pegshaped), each 0.6–2 mm in diameter, up to 1.3 mm high; petioles 1–6.3 cm long; stipules triangular to linear, eglandular. Flowers ca 12–20 per congested pseudoraceme, these borne in dichasia or small thyrses, rarely solitary. Peduncles 3–9 mm long, pedicels 2.5–9.5 mm long, terete, peduncles $\frac{1}{5}$ – $1\frac{4}{5}$ times as long as pedicels; bracts 0.8–1.8 mm long, triangular or narrowly so, bracteoles 0.9–1.5 mm long, triangular or broadly so, eglandular. Limb of anterior-lateral petals ca 5.5–7 mm long and wide, limb of posterior-lateral petals ca 4–5.5 mm long and wide, limb of posterior petal ca 3.5–5 mm long and wide, all orbicular, margin erose or erose-dentate, teeth up to 0.3 (–0.4) mm long. Stamens equal in shape, that opposite the anterior style usually the longest or those opposite the anterior-lateral sepals equally long; anthers equal in shape, subequal in size, glabrous. Anterior style 1.3–2.1 mm long, slightly shorter than or equal to the posterior two, glabrous; apex 0.7–0.9 (–1.2) mm long including a spur up to 0.2 mm long, linear, 0.2–0.3 (–0.4) mm wide, folioles absent. Posterior styles 1.6–2.4 mm long, glabrous, erect; apex 0.8–1.3 mm long including a spur up to 0.2 (–0.3) mm long or blunt, linear, 0.3–0.4 (–0.5) mm wide, folioles absent. Dorsal wing of samara 4–5.4 cm long, 1.5–2.3 cm wide, upper margin with a tooth; nut bearing 1–3 lateral winglets on each side or only 1–2 spurs and/or crests or with a network of prominent ribs up to 0.5 mm high; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower from May through February, in fruit from September through May and in July.

Distribution. Chiapas, Mexico, and Huehuetenango, Quetzaltenango, Suchitepéquez, and Alta Verapaz, Guatemala; upper elevation pine-oak forest and montane rain forest; (1000–) 1300–2700 m.

REPRESENTATIVE SPECIMENS. MEXICO. Chiapas: Mpio Zinacantán, along Mex. Hwy at paraje Sequentic, *Breedlove* 10395 (DS, F, MICH, US, UTD); Mpio Jitotol, 6.5 km N of Jitotol along road to Pichucalco, *Breedlove* 21417 (DS, ENCB, MICH, MO, NY); Mt. Male, near Porvenir, *Matuda* 4588 (A, F, MEXU, MO, NY, US); Mt. Ovando, *Matuda* 2661 (A, DS, F, MEXU, MICH, NY, US, UTD); Mpio La Trinitaria, Lagos de Montebello, E side of Lago Tsikaw, *Shilom Ton* 2643 (DS, ENCB, MICH, NY).—GUATEMALA. Alta Verapaz: Pansamalá, *von Türckheim* 708 (GH, NY, P, US). Huehuetenango: near Jacaltenango, *Steyermack* 51840 (F, US). Quetzaltenango: Chiquihuite, *Standley* 68103 (F). Suchitepéquez: flood plain of Río Mocá, *Skutch* 1578 (A, F, US).

Stigmaphyllon pseudopuberum is the only other species in our area besides the coastal *S. ovatum* in which the stamens and the styles are subequal. The styles are efoliolate; the anterior one always has a tiny spur, and the posterior styles may also have such a spur or be blunt. The small flowers are borne in crowded compound inflorescences.

This distinctive species has sometimes been confused with *S. puberum*, because they both commonly have elliptical to lanceolate laminas; neither species has cordate leaf blades, which are more common in the genus. In *S. pseudopuberum* the laminas are sericeous to often very densely so below; in *S. puberum* they are sericeous to sparsely so below. *Stigmaphyllon puberum* is easily separated by its flowers and samaras. The petals are fimbriate rather than erose or erose-dentate, and the stamens and the foliolate styles are unequal. In *S. pseudopuberum* the samara has a large, flaring dorsal wing; that of *S. puberum* has the dorsal wing encircling the nut and tapering distally. The two species are not sympatric. *Stigmaphyllon pseudopuberum* is an upland species, while *S. puberum* has not been recorded from elevations above 500 m.

***Stigmaphyllon puberum* (Rich.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 289.**

1840. *Banisteria pubera* Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792.—

TYPE: FRENCH GUIANA. *LeBlond* 44 (holotype: G!).

Stigmaphyllon puberum β *schomburgkianum* Bentham, London J. Bot. 7:

129. 1848.—TYPE: GUYANA. *Rob. Schomburgk 2nd. coll. 819 (1500)*

(holotype: K!; isotype: G!).

Laminas 8.2–20.2 cm long, (2–) 3–12.5 cm wide, commonly lanceolate or narrowly so (rarely linear-lanceolate) to elliptical to ovate to sometimes suborbicular, apex acuminate, base attenuate or truncate or sometimes cordate, glabrate or glabrous above, sericeous to sparsely so below, margin with scattered sessile glands, basal glands prominent, sessile, each 1–1.8 (–2.2) mm in diameter; petioles 1.2–7.2 cm long; stipules triangular to linear, eglandular. Flowers 8–15 per umbel, these born in dichasia or small thyrses, rarely solitary. Peduncles (0.8–) 1.5–4.8 mm long, pedicels 2.5–7.5 mm long, terete, peduncles $\frac{1}{5}$ – $\frac{5}{6}$ as long as the pedicels or rarely subequal; bracts 1.1–2.2 mm long, triangular or broadly so, bracteoles 0.8–1.4 mm long, broadly triangular to ovate or parabolic, eglandular. Limb of anterior-lateral petals ca 8–13 mm long and wide, limb of posterior-lateral petals ca 7–8.5 mm long and wide, all orbicular, margin with fimbriae up to 0.6 (–0.8) mm long; limb of posterior petal ca 5–7 mm long, 4.5–6.5 mm wide, orbicular to broadly obovate or sometimes almost square, margin with fimbriae up to 0.6 mm long. Stamens unequal, that opposite the anterior style the largest, those opposite the anterior-lateral sepals with the connective enlarged and the locules reduced; anthers glabrous. Anterior style 3.5–4.6 mm long, longer than the posterior two, glabrous or sometimes with scattered hairs in the proximal half; apex (1–) 1.2–1.8 mm long including a spur 0.1–0.3 mm long, each foliole (0.7–) 1–1.8 mm long, (0.6–) 1–1.5 (–1.7) mm wide, commonly narrowly trapezoidal or rectangular to subsquare. Posterior styles 2.5–3.3 (–3.5) mm long, glabrous or sometimes with scattered hairs in the proximal third, lyrate; folioles 0.9–1.5 mm long, 0.6–1.1 mm wide, rectangular to rhombic or sometimes triangular. Dorsal wing of samara 2.6–3.7 cm long, 0.9–1.5 cm wide, tapering from the nut and encircling it; nut smooth or sometimes with 1–5 prominent ribs; embryo ovoid, ca two times as long as wide.

Phenology. Collected in flower and fruit throughout the year.

Distribution. In Central America in the Atlantic lowlands and also in the Pacific lowlands of Costa Rica (Golfo Dulce area) and Panama, lowlands of northern South America, in the West Indies recorded from Jamaica (very rare, fide Adams, 1972), the Dominican Republic, Puerto Rico, Guadeloupe, Désiderade, Martinique, Dominica, and St. Vincent; in wet areas: rain forests, gallery forests, river banks, and mangrove swamps; sea level to 500 m.

REPRESENTATIVE SPECIMENS. JAMAICA. *McNab s.n.* (GOET).—DOMINICAN REPUBLIC. Santo Domingo, Llano Costero, *Ekman H12508* (F, G, MICH, NY, S, US); prov. Samaná, Sánchez, in the Gran Estero, *Ekman 14796* (S).—PUERTO RICO. Colonia Paraíso, *Liogier et al. 30076* (NY, UPR); at KM 28.1 on rte 191 near Florida, *Wagner 1643* (A, U mixed with *S. emarginatum*).—GUADELOUPE. *Duss 2414* (F, MO, NY, US); *Stehlé 410* (P, S, US).—DOMINICA. *Eggers 651* (BR, G, GH, GOET, M, P, W); *Hodge 554* (GH, NY); *Howard 11761* (A, NY).—MARTINIQUE. *Duss 1472* (F, GH, MO, US); *Hahn 1132* (BR, G, P, W); *Stehlé & Stehlé 4506* (US).—ST. VINCENT. *Smith & Smith 1261* (NY).—BELIZE. Toledo: Monkey River, *Gentle 3567* (MICH, MO, NY, U, US, UTD); “El Dorado,” Punta Gorda, *Schipp 1009* (A, CAS, F, G, GH, MICH, MO, NY, S).—GUATEMALA. Izabal: S of Río Dulce, *LeDoux et al. 2094* (CAS, LL, MEXU, MICH, MO, NY, WIS); vic. of Quiriguá, *Standley 24059* (GH, NY, US). Petén: Cadenas, *Contreras 9155* (LL, MICH, UTD).—HONDURAS. Atlántida: between Tela and Lancetilla, *Yuncker 4577* (A, F, MICH); vic. of La Ceiba, along Río Danto, slopes of Mt. Cangrejal, *Yuncker et al. 8434* (F, G, GH, MICH, MO, NY, S, US). Cortés: Golfo de Honduras, 2 mi W of Omoa, *Webster et al. 12715* (F, MO).—NICARAGUA. Río San Juan: Río Indio, 5 hrs upriver from San Juan del Norte, 11°07'N, 83°50–52'W, *Riviere 242* (MO). Zelaya: Isla del Maíz Grande, *Martínez S. 1696* (MICH); Río Chiquito, Caño Dos Oros, a 5–7 km al N de Atlanta, *Téllez et al. 4950* (MO).—COSTA RICA. Heredia: Finca La Selva, OTS Field Station, Río Viejo just E of its junction with the Río Sarapiquí, *Hammel 9325* (DUKE); near Puerto Viejo de Sarapiquí, *Murray & Johnson 881* (MICH). Limón: ca 1 km N of Cahuita, *Almeda 3245* (CAS, MICH); banks of the Río Colorado, *Morley 803* (F, GH, MO, US); northern outskirts of Cahuita, ca 47 km S of Limón, *Wilbur et al. 23362* (MICH, DUKE). Puntarenas: Golfito de Osa, *Brenes 12292* (no. 75 of the Porsch Expedition) (F, W); Corcovado Natl Park, 0–2 km W of park headquarters at Sirena, 8°29'N, 83°36'W, *Liesner 2910* (MO); Santo Domingo de Golfo Dulce, *Tonduz 6985* (F, GH, MICH, US), 9942 (BR, P).—PANAMA. Bocas del Toro: Río San Pedro, *Gordon 84C* (MO); Water Valley, *von Wedel 2662* (GH, MO, NY); vic. of Chiriquí Lagoon, *von Wedel 2761* (GH, MO, NY). Canal Zone: Juan Mina, *Bartlett & Lasser 16510* (MICH, MO); near Gamboa, *Clewell & Tyson 3267* (MO); Barro Colorado Island, *Bangham 496* (A, F, S), *Foster 1033* (F, DUKE). Colón: Coclé del Norte, *Hammel 4583* (MICH); Quebrada Santa Marta, on coast rd, 4.5 km SW of PINA, *Nee 11716* (MICH, MO); N of Río Guanche, *Davidse & D'Arcy 10070* (MO, NY). Darién: Río Ucuquantí, *Bristan 1154* (MO); Río Tuirá, between Río Purnusa and Río Mangle, *Duke 14611* (MO); Ensenada del Guayabo, 16–19 km SE of Jaqué, *Garwood 987* (MICH). Panamá: Río Mamoni, below La Caitana, *Pittier 4580* (F, GH, S). San Blas: Mulatuppu, Río Ibadi, *Duke 8474* (MO); mainland opposite Playon Chico, *Gentry 6408* (MICH); Ailigandí, *Hammel & D'Arcy 4965* (MO).

In *S. puberum*, as in *S. hypargyreum*, the anterior style and its opposing stamen are larger than the posterior styles and their opposing stamens. In all other species in our area, the posterior styles and their stamens exceed or at least are equal to the anterior style and stamen. *Stigmaphyllon puberum* also differs from most species in its leaves, which are commonly lanceolate and always acuminate. The petals are fimbriate. The samara is unusual in that the dorsal wing encircles the nut and tapers distally. In flower *S. puberum* might be confused with *S. hypargyreum*, but in that species the laminae are so densely silvery sericeous below that the epidermis is obscured, and the petals are erose to denticulate or if fimbriate with fimbriae only up to 0.2 (–0.3) mm rather than 0.6 (–0.8) mm long.

Stigmaphyllon retusum Griseb. in Oersted, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjobenhavn 1853(1–2): 45. 1854.—TYPE: NICARAGUA. “Prope Granada,” *Oersted s.n.* (lectotype, here designated: GOET!; isolectotype: C!).

Stigmaphyllon lupulus S. Watson, Proc. Amer. Acad. Arts 21: 461. 1886.

Stigmaphyllon lindenianum var. β . *lupulus* (S. Watson) Nied., Ind. Lect. Lyc. Brunsbergi p. aest. 1900: 19. 1900. *Stigmaphyllon lindenianum* subsp. *lupulus* var. γ . *watsonianum* Nied., Pflanzenreich IV. 141(2): 499. 1928, nom. superfl.—TYPE: GUATEMALA. Izabal: Chocón, 21 Mar 1885, Watson 35 (holotype: GH!).

Stigmaphyllon lindenianum var. γ . *nicaraguense* Nied., Ind. Lect. Lyc. Brunsbergi p. aest. 1900: 19. 1900.—TYPE: NICARAGUA. Wright s.n. (holotype: B, destroyed; isotypes: GH! GOET! US!).

Laminas 7–18 cm long, 5–15 cm wide, triangular to cordate to ovate to elliptical or sometimes 3(–5)-lobed or rarely suborbicular, apex mucronate or acuminate-mucronate, base cordate or sometimes truncate, glabrate to glabrous above, with T-shaped hairs and/or tomentose below, margin with scattered sessile glands and sometimes also with scattered filiform glands up to 2.5 (–5.5) mm long, basal glands prominent, sessile, each 1.2–2.7 mm in diameter; petioles 1.6–9.5 cm long; stipules triangular, eglandular. Flowers 15–35 (–40) per umbel or corymb, these borne in dichasia or compound dichasia or small thyrses, rarely solitary. Peduncles 2.5–8.5 (–10) mm long, pedicels 4–10 mm long, terete, peduncles $\frac{1}{2}$ as long as to subequal to the pedicels; bracts 0.8–2.1 mm long, triangular to narrowly so, bracteoles 0.5–1.5 (–1.8) mm long, triangular to parabolic to oblong to subsquare, eglandular. Limb of anterior-lateral petals 7–13.5 mm long, 7–12 mm wide, limb of posterior-lateral petals ca 5.5–11 mm long, ca 5–10.5 mm wide, all orbicular to broadly obovate, margin erose or denticulate or denticulate-fimbriate or with fimbriae up to 0.3 mm long; limb of posterior petal 5.5–9.5 mm long, 4.5–7 mm wide, broadly elliptical to obovate to suborbicular, margin denticulate or denticulate-fimbriate or with fimbriae up to 0.3 (–0.4) mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the anterior-lateral sepals sometimes equally long, those opposite the lateral sepals with the connective enlarged and the locules reduced (sometimes only slightly reduced in stamens opposite the anterior-lateral sepals); anthers pubescent. Anterior style 1.8–3 mm long, shorter than the posterior two or sometimes almost as long, glabrous; apex 0.8–1.5 mm long, each foliole 0.5–1.6 mm long and wide, parabolic to rectangular to square, folioles rarely unequal, rarely one or both folioles reduced and the apex merely expanded, ca 0.6 mm wide. Posterior styles 2.4–3.8 (–4) mm long, glabrous, lyrate; folioles (0.7–) 1–2.5 mm long and wide, square to subrectangular. Dorsal wing of samara 2.5–4.5 (–4.8) cm long, 1–1.5 (–1.8) cm wide, upper margin with a tooth; nut with a pair of lateral winglets and/or bearing spurs and/or crests or only prominently ribbed; embryo ovoid, ca two times as long as wide. Fig. 5a–h.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Southeastern Mexico to Nicaragua; in rain, evergreen, gallery, and scrub forests, in acahuals and matorrales, along rivers, in thickets, and at roadsides; sea level to 1100 m.

REPRESENTATIVE SPECIMENS. MEXICO. Chiapas: Mpio Palenque, 3–5 km N of Palenque along rd to Villahermosa, *Breedlove* 26648 (DS, MEXU, MO); Mpio La Independencia, valley of Santa Elena along rd to Ixcan, *Breedlove* 41958 (DS, MEXU, MICH); Mpio La Libertad, 10 km towards Chancala on rd to Bonampak, *Breedlove* 57845 (CAS). Oaxaca: Cerro Blanco, Teotitlán, *Conzatti* 3437 (MEXU, US); Tuxtepec, Chiltepec, *Martínez Calderón* 45 (CAS, CHAPA, ENCB, NY, TEX). Puebla: 5 km adelante de Ceiba Grande, orillas del Río Cazones, *Riba* 422B (ENCB); adelante de

Agua Fría, *Sarukhan et al.* 3250 (MEXU). San Luis Potosí: Tamazunchale, *Fisher* 3784 (GH, MO, NY, US); Mpio Valles, 1 km N of la Estribera, *Fryxell & Anderson* 3522 (MICH); near Tamasopo, *Pringle* 4102 (BR, F, G, GH, GOET, LL, M, MEXU, MICH, MO, MSC, NY, P, US, W). Veracruz: Mpio Cosamaloapan, Otatitlán, *Martínez C.* 1060 (CAS, ENCB, F, GH, MEXU, MO, NY); Atoyac, *Matuda* 1482 (MEXU, MICH, MO, NY, US); Mpio Martínez de la Torre, San Carlos, *Ventura A.* 1296 (DS, ENCB, F, MICH, MO).—BELIZE. El Cayo: Vaca, *Gentle* 2490A (MEXU, MICH, NY, UTD). Toledo: near Jacinto Hills, *Gentle* 5525 (LL, MICH, UTD).—GUATEMALA. Alta Verapaz: Chahal, on Sebol rd, *Contreras* 7759 (LL, MICH, UTD); SW of Lanquín, *Steyermark* 44074 (F, GH). Chiquimula: 2 km from Esquipulas, *Molina R. & Molina* 25197 (F, NY, US). Izabal: Cienaga, on Petén-Guatemala rd, *Contreras* 10825 (LL, MEXU, MO, S, US, UTD); 12 km N of Río Dulce on rd to Modesto Méndez, *Harmon* 2487 (F, MICH, MO). Jutiapa: near El Molina (dept. Santa Rosa), *Standley* 78475 (F). Petén: KM 158 on Cadenas rd, *Contreras* 6559 (LL, MICH, UTD). Retalhuleu: vic. of Retalhuleu, *Standley* 88789 (F). Santa Rosa: about Guazacapán, *Standley* 78593 (F).—HONDURAS. Comayagua: vic. of Siguatepeque, *Standley & Chacón* 6906 (F). Gracias a Dios: Río Plátano, *Gentry et al.* 7522 (F, MO). Morazán: drainage of Río Yeguaré, 14°N, 87°W, faldas del Cerro Majicarán, *Molina R.* 1756 (F, MO). Olancho: camino a San Francisco La Paz, matorral del Río Telica, *Molina R.* 13362 (F, NY).—EL SALVADOR. Ahuachapán: vic. of Ahuachapán, *Standley* 20347 (GH, NY, US). San Salvador: vic. of San Salvador, *Standley* 19643 (GH, NY, US). San Vicente: vic. of San Vicente, *Standley* 21272 (GH, NY, US).—NICARAGUA. Boaco: Camouapa, *Atwood* 3513 (F, GH, NY). Carazo: Río Grande, ca 4 km al N del balneario de Casares, *Grijalva & Vanegas* 3416 (MICH). Chinandega: Chinandega, *Baker* 2026 (A, F, G, GH, MO, MSC, NY, P, US, W). Chontales: Hacienda San Martín, near confluence of Río El Jordán and Río La Pradera, 12°17'N, 85°15'W, *Stevens* 22858 (MICH). Estelí: 3–7 km NW of Pueblo Nuevo, *Williams & Molina R.* 42391 (F, MICH, US). Granada: Volcán Mombacho, 1.3 km antes de Hacienda Cutirre, “El Cacao,” 11°51'N, 85°57'W, *Moreno* 6326 (MICH). Jinotega: al NE de Wiwilí, camino entre Carmen y Wamblán, ca 1 km al N del Carmen, 13°43'N, 85°46'W, *Araquistain & Moreno* 1505 (MICH). León: Volcán Momotombo, alrededores del Proyecto Geotermico, *Araquistain & Moreno* 1083 (MICH). Madriz: a 10.5 km al S de Somoto, carretera Panamericana, en el valle de Yalaguina, 13°30'N, 86°30'W, *Moreno* 5992 (MICH). Managua: ca 5 km NNW of Hwy 12 along rd on ridge of Sierra de Mateare, ca 12°07'N, 86°23'W, *Stevens* 6198 (MICH). Matagalpa: along Río Las Cañas, 10–15 km NE of Matagalpa, *Williams et al.* 24020 (F, NY). Masaya: a orillas de la Laguna Masaya, 11°58'N, 86°08'W, *Moreno* 6137 (MICH). Nueva Segovia: El Jícaro “Casas Viejas,” 13°45'N, 86°06'W, *Moreno* 5716 (MICH). Rivas: Isla Ometepe, Volcán Concepción, poblado La Esperanza, 11°31'N, 85°37'W, *Robledo* 1613 (MICH). San Juan del Norte: “El Carmen,” 2 km al N de San Miguelito, 11°25'N, 84°53'W, *Moreno* 23468 (MO). Zelaya: along new rd to Mina Nueva America, leading ca W from 14.3 km N of El Empalme on main rd to Rosita, *Stevens* 12705 (MICH).

Stigmaphyllon retusum is a widespread, highly polymorphic species, whose stem and leaf vesture is composed of T-shaped hairs and whose anthers are pubescent. The leaves vary from triangular to cordate to ovate to elliptical or sometimes are 3–5-lobed or rarely suborbicular. The name *S. retusum* has never been taken up, and these plants have usually been reported as *S. lindenianum* and *S. humboldtianum*. In *S. lindenianum* the leaves are always sericeous or sparsely so below. *Stigmaphyllon humboldtianum* has glabrous anthers and occurs in our area only in Darién, Panama.

Plants from Veracruz and adjacent San Luis Potosí, Puebla, and Oaxaca, Mexico, are most similar to those from southern Guatemala to Nicaragua. The limbs of the lateral petals are 6.5–9.5 mm long, and the limb of the posterior petals is ca 6–8 mm long. The folioles of the anterior style are 0.5–1.5 mm long and 0.5–1.2 mm wide, and are inserted at about the center of the apex of the style. The folioles of the posterior styles are ca 1–1.6 mm long and ca 1–1.9 mm wide. Flowers of the Mexican plants tend to be at the larger end of the range of these measurements and those of the southern plants at the smaller end. In the Mexican specimens the hairs on the branches and petioles tend to be stiffer and have slightly longer stalks, 0.2–0.3 (–0.4) mm long, than those of the southern Guatemalan to Nicaraguan ones in which the stalks are 0.1–0.3 (–0.4) mm long.

The samaras of the Mexican plants have the dorsal wing 2.5–3.1 cm long; the nut commonly bears 2–3 lateral winglets per side or sometimes only crests and/or spurs or is only prominently veined. In samaras from southern Guatemala to Nicaragua the dorsal wing is 3.5–4.5 cm long; the nut usually bears 3–5 lateral winglets per side.

Plants from Chiapas, Mexico, Belize, and northern Guatemala (Petén, Izabal, and Alta Verapaz) are usually larger in most aspects than plants from the rest of the range. The limbs of the lateral petals are 9.5–13.5 mm long and the limb of the posterior petal is 8.5–9.7 mm long. The folioles of the anterior style are usually 1.3–1.7 mm long and 1.1–1.5 mm wide, and are inserted adjacent to the stigma. The folioles of the posterior styles are 2.2–2.5 mm long and 2.1–2.3 mm wide. The hairs tend to be stiff and have a stalk 0.2–0.5 mm long. The samaras have large dorsal wings, 3.5–4.1 (–4.8) cm long, like those of specimens from southern Guatemala to Nicaragua, but the nut usually is prominently ribbed or bears small crests and/or spurs and only infrequently lateral winglets. These plants were recognized by Watson as *S. lupulus* and by Niedenzu as a variety and later as a subspecies. Most of these plants are separable from *S. retusum* from other parts of the range, but the separation is quantitative rather than qualitative and not consistent; they should not be accorded taxonomic status. Individuals with large flowers and/or samaras and/or long-stalked hairs do occur in the northern and more southern part of the range; individuals with smaller flowers and samaras and short-stalked hairs are rare but not absent in the central part (*Breedlove* 57845). Niedenzu also noted this diversity and recognized Nicaraguan plants as a variety of his subsp. *lupulus*.

Stigmaphyllon sagraeanum Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290. 1840.

Stigmaphyllon sagraeanum f. *I. typicum* Nied., Pflanzenreich IV. 141(2): 482. 1928.—TYPE: CUBA. *de la Sagra s.n.* (holotype: P–JU!).

Stigmaphyllon reticulatum Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 290.

1840. *Stigmaphyllon sagraeanum* f. 2. *reticulatum* (Adr. Juss.) Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 11. 1899.—TYPE: CUBA. *de la Sagra s.n.* (lectotype, here designated: P–JU!).

Stigmaphyllon obtusum Turcz., Bull. Imp. Soc. Naturalistes Moscou 35: 583.

1863.—TYPE: CUBA. *de la Sagra s.n.* (holotype: CW?).

Stigmaphyllon faustinum Wright in Sauv., Anales Acad. Ci. Méd. Habana 5:

244. 1868. *Stigmaphyllon sagraeanum* f. 4. *faustinum* (Wright in Sauv.) Nied., Ind. Lect. Lyc. Brunsberg. p. hiem. 1899–1900: 11. 1899.—TYPE: CUBA. *Wright 3522* (holotype: HAB?; isotypes: NY! US!).

Stigmaphyllon sagraeanum f. 3. *wrightianum* Nied., Ind. Lect. Lyc. Bruns-

berg. p. hiem. 1899–1900: 11. 1899.—TYPE: CUBA. *Wright 2154 p.p.* (holotype: B, destroyed; isotype: G!).

Stigmaphyllon sagraeanum f. 5. *primaevum* Nied., Verz. Vorles. Ak. Brauns-

berg W.-S. 1912–1913: 26. 1912.—TYPE: CUBA. Pinar del Río, *Baker & Abarca 3699* (*Herb. Est. Centr. Agr.*) (holotype: B, destroyed; isotype: NY!).

Stigmaphyllon coccolobaefolium Alain, Phytologia 8: 369. 1962.—TYPE:

CUBA. Oriente: Vía Sur, near Yateritas, on coastal rocks, 10 Jan 1956, *Alain & Morton 4955* (holotype: NY!; isotypes: LS, SV, fide Alain).

Stigmaphyllon nipense Alain, Bull. Torrey Bot. Club 90: 188. 1963.—TYPE:

CUBA. Oriente: Sierra de Nipe, in charrascales, 300–400 m, 7 Jan 1956, *Morton et al. 8784* (holotype: US!).

Laminas (1–) 2.9–13 cm long, 0.2–7 cm wide, linear to oblong to lanceolate to elliptical to suborbicular, apex mucronate or mucronate-emarginate, base truncate or slightly cordate, glabrate to glabrous above and below, margin eglandular, basal glands usually stipitate and up to 1 (–2) mm long or sometimes sessile, each 0.2–1 mm in diameter, or sometimes one or both glands absent; petioles (1.6–) 2.2–6 cm long; stipules narrowly triangular, eglandular. Flowers (8–) 20–25 (–50) per umbel or pseudoraceme, sometimes a corymb, these solitary or borne in compound dichasia or small thyrses. Peduncles absent to 9 mm long, pedicels (8.5–) 12–27 mm long, terete, peduncles if present always much shorter than the pedicels; bracts (0.6–) 1–2 mm long, narrowly triangular, bracteoles 0.6–1 (–1.4) mm long, narrowly triangular, eglandular. Limb of lateral petals 8–10.5 mm long and wide, limb of posterior petal 6.5–7 mm long and wide, all orbicular or suborbicular, margin erose. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals with the connective enlarged and the locules reduced, rarely those opposite the posterior-lateral sepals with only one locule or sterile; anthers glabrous. Anterior style (2.6–) 3–3.6 mm long, shorter than the posterior two, glabrous; apex 0.7–0.9 mm long including a spur 0.3–0.5 mm long, linear, 0.3–0.4 mm wide, folioles absent. Posterior styles 3.3–4 mm long, glabrous, lyrate; folioles 0.9–1.3 mm long, 0.4–0.8 mm wide, oblong to parabolic, or sometimes the foliole reduced to a narrow lip, or rarely absent and apex ca 1 mm long including a spur 0.3–0.4 mm long, linear, ca 0.2 mm wide. Dorsal wing of samara 1.8–2.4 cm long, 0.7–1.5 cm wide, upper margin with a tooth; nut with prominent veins; mature seed not seen.

Phenology. Collected in flower and fruit throughout the year.

Distribution. Cuba and the Bahamas; on limestone and serpentine outcrops, in coastal thickets, open savannas, and pastures; sea level to 1200 m.

REPRESENTATIVE SPECIMENS. BAHAMAS. Andros Island: *Correll & Godfrey 41259* (LL, MO, NY); *Small & Carter 8441* (F, NY); *Wight 236* (F, GH, NY). Eleuthera: *Correll & Hill 45231* (NY). Long Island: *Britton & Millspaugh 6232* (F, NY); *Correll 44863, 48173* (NY). Rum Cay: *Gillis 6240, 6262* (MSC).—CUBA. Camagüey: 6 mi NW of Cayo Coco, *Shafer 2692* (NY, US); La Gloria, *Shafer 176* (NY, US); Atalaya, *Shafer 979* (NY); S of Sierra Cubitas, *Shafer 497* (NY). Havana: vic. of Cojimar, *Britton et al. 6230* (NY); San Antonio, *van Hermann 834* (F); El Morro to Cojimar, *Wilson 9133* (NY); Havana, *Shafer 542* (CM, NY); Isla de Pinos, *Curtiss 213* (A, CM, F, G, M, MO, NY); *Jennings 1* (NY), *33* (NY), *520* (CM); *Killip 41660* (GH), *43560* (P), *43599* (GH); *Millspaugh 1419* (F). Mantanzas: vic. of Mantanzas, gorge of the Yumuri, *Britton et al. 496* (CM, F, NY); Mantanzas, *Rugel 157* (GH, MO, NY), *Britton et al. 71* (CM, NY), *Ekman 17212* (A, S). Oriente: Río Macaguani-gua, *Shafer 3937* (NY, US); Gibara, *Pollard et al. 5* (A, CM, F, GH, MO, NY, US); valley of Río Bayamita, S slope of Sierra Maestra, *Maxon 3912* (F, GH, MO, NY, US); Baracoa, *Underwood & Earle 1353* (NY); Punta Piedra, Nipe Bay, *Britton et al. 12454* (NY, US); Bayate, Sabana Resueña, *Ekman 2819* (NY, S). Pinar del Río: Bahía Honda, *Wilson 9418* (NY, U); Sierra de Anafe, *Wilson 11431* (NY); Buenaventura to San Juan de Guacamalla, *Wilson 9321* (NY); Laguna Jovero to Las Martinas, *Shafer 11034* (F, MO, NY). Las Villas: 12 km E of Cascajal, *Howard 5586* (GH, NY); Río Toyaba, Trinidad, *Britton et al. 5550* (NY); Trinidad, La Viga hill, *Britton & Wilson 5530* (NY); Río San Juan, *Britton et al. 5883* (NY). Without locality: *Wright 97* (BR, G, GH, GOET, LE, MO, NY, P, S, W).

In *S. sagraeanum*, as in the West Indian *S. diversifolium* and *S. emarginatum*, the laminas vary from linear to suborbicular; most commonly they are elliptical to broadly linear-oblong and are rugose and glabrous. The basal leaf glands are usually peg- or sometimes nail-like. The peduncles are always much shorter than the pedicels or sometimes absent.

Stigmaphyllon sagraeanum is the only species in the West Indies in which the anterior style lacks folioles but the posterior styles bear them; however, the size

of the folioles is variable. In the majority of specimens the folioles are broadly oblong to parabolic, but in a number of individuals the folioles are reduced and narrowly triangular or may be represented only by a lip. A collection from the province of Havana (*van Hermann* 834) even has a flower in which one posterior style has a large foliole and the other one only a tiny flap. In some specimens, from various parts of Cuba, the posterior styles lack folioles. The styles are efoliolate and subequal in all collections seen from the Sierra de Nipe (Oriente) and in all but two from the Isla de Pinos; the posterior styles of the two exceptions (*Jennings* 1, 33; both NY) have large folioles. This extreme reduction was recognized as f. *primaevum* by Niedenzu, who considered the efoliolate condition ancestral. Such variability and even loss of the foliole is also known in other species. Because the degree of reduction is greatly variable, and because it is the only character in which these individuals differ from the typical representatives of *S. sagraeanum*, these plants are not recognized taxonomically here. Future work with living plants may reveal that the loss of the folioles is genetically fixed and should be accorded varietal or even specific status.

Stigmaphyllon selerianum Nied., Ind. Lect. Lyc. Brunsberg. p. aest. 1900: 7. 1900.—TYPE: MEXICO. Oaxaca: Distr. Nochixtlán, Almoloyas, 15 Nov 1895, *Seler & Seler* 1374 (holotype: B, destroyed, fragment: NY!, photos: A! F! MICH! NY!).

Laminas 4–17.5 cm long, 3–15 cm wide, cordate or narrowly so, apex mucronate or emarginate-mucronate, base auriculate, glabrous above, sparsely sericeous to glabrate below, margin with cilia up to 0.8 mm long, basal glands prominent, sessile, each 1–2.8 mm in diameter; petioles 1.5–7 cm long; stipules triangular or sometimes oblong, eglandular. Flowers 8–12 per umbel or corymb or sometimes a pseudoraceme, these solitary or borne in dichasia or rarely in small thyrses. Peduncles 0.5–3 mm long, pedicels 6.5–11.5 mm long, terete, peduncles up to $\frac{1}{3}$ as long as pedicels; bracts 1–2 mm long, broadly triangular, bracteoles 0.9–1.9 mm long, broadly triangular, eglandular. Limb of anterior-lateral petals ca 11.5–13 mm long, ca 10–13 mm wide, limb of posterior-lateral petals 8.5–11.5 mm long and wide, all broadly elliptical to orbicular, margin erose; limb of posterior petal 8.5–9.5 mm long, 7–8.5 mm wide, broadly elliptical or broadly obovate to sometimes orbicular, margin erose or denticulate-fimbriate, teeth and fimbriae up to 0.5 mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the lateral sepals sometimes with the connective enlarged and the locules reduced; anthers glabrous or the largest sometimes with scattered hairs. Anterior style 2.5–3 mm long, at least slightly shorter than the posterior two, glabrous; apex 1.3–1.6 mm long including a spur 0.4–0.8 mm long, linear or elliptically to obovately expanded distally, folioles absent. Posterior styles 2.8–3.5 mm long, glabrous, lyrate; apex 1.3–1.9 mm long, abaxially laterally expanded into a lip or semielliptical foliole 0.5–1.3 mm wide. Dorsal wing of samara ca 3.5–4 cm long, ca 1.1–1.5 cm wide, upper margin with a tooth; nut smooth or bearing a spur or winglet; mature seed not seen.

Phenology. Collected in flower in June and from September through March, in fruit in December, January, and March.

Distribution. Endemic to Oaxaca and Chiapas, Mexico; in evergreen and tropical deciduous forest, and in thickets on limestone hills; 550–1500 m.

SPECIMENS EXAMINED. MEXICO. Chiapas: 11 mi from El Sumidero on road to Tuxtla Gutiérrez, *Anderson & Anderson 5555* (ENCB, MICH); Mpio Tuxtla Gutiérrez, on road to El Sumidero, 8 km N of Tuxtla Gutiérrez, *Breedlove 9027* (DS, F); Mpio Jiquilpas, 20 km N of Jiquilpas and Mex Hwy 190, *Breedlove 24135* (MEXU, MICH, MO, NY, UTD); Mpio La Trinitaria, 18 km S of La Trinitaria on road to Colonia Morelos and Colonia Chihuahua, *Breedlove 46460* (CAS); Mpio Villa Corzo, 32 km from Tuxtla along rd to Nueva Concordia, *Breedlove 48714* (CAS); Mpio Chiapa de Corzo, above El Chorreadero, *Breedlove 50177* (CAS); Trapichito Comitán, *Matuda 5686* (F, MEXU, UTD). Oaxaca: de Almoloyas a Santa Catarina, *Conzatti 1680* (NY, US); Dominguillo, *Miranda 1016* (MEXU); Río de las Vueltas, Dominguillo, *Miranda 4731* (MEXU); Tomellin Canyon, *Pringle 5972* (GH, MICH, US); Nochixtlán, *Quarles van Ufford 348* (U); Jacatlán, *Smith 531* (US).

Stigmaphyllon selerianum is distinguished by the cordate or narrowly cordate leaves, which are fringed with filiform glands. The only other species in our area with ciliate leaves is the coastal *S. ciliatum*, whose leaves are so deeply auriculate that the lobes overlap. It also differs in its larger flowers with foliolate styles, inflated pedicels, and lenticular samaras. In *S. selerianum* the anterior style is efoliolate and the posterior styles have a lateral lip or a small foliole; the pedicels are terete, and the samaras are typical for the genus. *Stigmaphyllon selerianum* is most likely to be confused with *S. cordatum*, an endemic of the highlands of eastern Guatemala; see that species.

Stigmaphyllon tonduzii C. Anderson, sp. nov.—TYPE: COSTA RICA. Guanacaste: Playa Tamarindo, 19 Feb 1985, *Frankie s.n.* (holotype: MICH).

Liana. Laminae 9.5–12 cm longae, 9–12 cm latae, ellipticae vel interdum 3–5-lobatae, supra sericeae vel glabratae, subtus pilos T-formes ferentes, margine glandulosae. Inflorescentia dichasialis vel thyrsiformis constata ex umbellis, floribus in quaque umbella ca 12–20. Pedunculi 3.5–8.5 mm longi; pedicelli 4–7 mm longi. Bracteae 0.8–1.5 mm longae, triangulares; bracteolae 0.8–1.2 mm longae, oblongae vel ovatae, eglandulosae. Petala lateralia orbicularia vel suborbicularia, marginibus erosis; petalum posticum ovatum vel late ellipticum vel orbiculare, margine eroso-denticulata vel eroso-fimbriata. Stamina heteromorpha, omnia fertilia vel antherae petalis postico-lateralibus oppositae raro steriles; antherae glabrae. Stylus anticus 2.6–3.2 mm longus, apice 1.3–1.6 mm longo, utroque foliolo 1.2–1.5 mm longo, 1.4–1.6 mm lato, subquadrato; styli postici 3.3–3.6 mm longi, lyrati, foliolo ca 1.7 (–2.4) mm longo, 1.8–2.3 mm lato, quadrato vel subrectangulari.

Laminas 9.5–12 cm long, 9–12 cm wide, elliptical or sometimes 3–5-lobed, apex acuminate or acuminate-mucronate, base slightly cordate to truncate, sparsely sericeous to glabrate above, with T-shaped hairs to tomentose below, margin with scattered sessile glands, basal glands prominent, sessile, each 1–1.7 mm in diameter; petioles 2–5 cm long; stipules triangular, eglandular. Flowers ca 12–20 per umbel, these borne in dichasia or small thyrses. Peduncles 3.5–8.5 mm long, pedicels 4–7 mm long, terete, peduncles $\frac{2}{3}$ – $1\frac{3}{4}$ times as long as pedicels; bracts 0.8–1.5 mm long, triangular, bracteoles 0.8–1.2 mm long, oblong or ovate, eglandular. Limb of anterior-lateral petals 10–10.5 mm long and wide, limb of posterior-lateral petals 7.5–9 mm long and wide, all orbicular or suborbicular, margin erose; limb of posterior petal 6.5–8 mm long, 6–7 mm wide, ovate to broadly elliptical to orbicular, margin erose-denticulate or erose-fimbriate, fimbriae up to 0.3 (–0.5) mm long. Stamens unequal, those opposite the posterior styles the largest, sometimes those opposite the anterior-lateral sepals equally

long, those opposite the lateral sepals with the connective enlarged and the locules reduced or those opposite the posterior-lateral sepals with only one locule or sometimes sterile; anthers glabrous. Anterior style 2.6–3.2 mm long, shorter than the posterior two, glabrous; apex 1.3–1.6 mm long, each foliole 1.2–1.5 mm long, 1.4–1.6 mm wide, subsquare. Posterior styles 3.3–3.6 mm long, glabrous, lyrate; folioles ca 1.7 (–2.4) mm long, 1.8–2.3 mm wide, square to subrectangular. Dorsal wing of samara 2.3–3 cm long, 0.7–1 cm wide, upper margin with a tooth; nut smooth or bearing spurs and/or crests; embryo ovoid, ca two times as long as wide. Fig. 6m–o.

Phenology. Collected in flower and fruit in February and in April.

Distribution. Guanacaste (Nicoya peninsula) and eastern Puntarenas, Costa Rica; dry open woods, scrub, and thickets; sea level to ca 100 m.

ADDITIONAL SPECIMENS EXAMINED. COSTA RICA. Guanacaste: Playa Tamarindo, 18 Feb 1985, *Frankie s.n.* (MICH); Nicoya, *Tonduz 13479, 13824* (US); San Isidro, Nicoya, *Tonduz 14008* (US). Puntarenas: Hwy 1 W of San José, KM 135, *Meerow et al. 1003* (SEL).

Stigmaphyllon tonduzii is characterized by elliptical or sometimes lobed leaves that bear T-shaped hairs below and by relatively large flowers with foliolate styles. The anthers are glabrous, and those of the stamens opposite the posterior-lateral sepals are sometimes sterile. This species is most likely to be confused with the variable *S. retusum*, whose range extends from Mexico to Nicaragua, and *S. lindenianum*, which occurs in Costa Rica in the Atlantic lowlands and the Osa Peninsula. Both species have pubescent and always fertile anthers. *Stigmaphyllon lindenianum* also differs in that its leaves are sericeous below. *Stigmaphyllon tonduzii* also resembles *S. humboldtianum*, a species of northern South America that extends into southern Panama. They differ most strikingly in the embryo, which is flattened in *S. humboldtianum* but ovoid in *S. tonduzii*. The samaras are larger in *S. humboldtianum*. The flowers are smaller than those of *S. tonduzii*, with the posterior petal always fimbriate, and are aggregated in clusters of 15–40 (–50). In *S. tonduzii* the margin of the posterior petal varies from erose-denticulate to erose-fimbriate, and the flowers are borne in ca 12–20-flowered umbels.

This species is named for Adolphe Tonduz (1862–1921), who first collected it on the Nicoya peninsula.

EXCLUDED AND DOUBTFUL NAMES

Stigmaphyllon palmatum (Cav.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 288. 1840. *Banisteria palmata* Cav., Diss. 9: 430, t. 257. 1790.—TYPE: "Santo Domingo," *Desportes s.n.* (holotype: P–JU!).

Stigmaphyllon sagittatum (Cav.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13: 288. 1840. *Banisteria sagittata* Cav., Diss. 9: 430, t. 257. 1790.—TYPE: "Santo Domingo," *Desportes s.n.* (holotype: P–JU!).

These names apply to a South American species that does not occur on Hispaniola or elsewhere in the West Indies. The type specimens were probably collected in French Guiana.

Stigmaphyllon lineare var. *morroensis* Kitanov, God. Sofijsk. Univ. 66: 4. 1974.—TYPE: CUBA. Oriente: Lomas cerca del Morro, Santiago de Cuba, 24 Aug 1952, *Lopes Figueiras s.n.* (holotype: SV–624, fide Kitanov).

Stigmaphyllon sagraeanum var. *angustiifolium* Kitanov, God. Sofijsk. Univ. 66: 4. 1974.—TYPE: CUBA. Oriente: Matanzas Cuabal del Espinal, Canasi, *Acuña & León* 22847 (holotype: SV, fide Kitanov).

Unfortunately, I have not seen the types for these names, which probably apply to narrow-leaved forms of *S. sagraeanum*; the first name may apply to *S. diversifolium*. Only leaf characters are mentioned in the very brief descriptions. Without characterization of the styles and androecium, it is impossible to assign these names to either species.

ACKNOWLEDGMENTS

I thank C. D. Adams, Rupert C. Barneby, Alan J. Bornstein, Gordon W. Frankie, Shirley A. Graham, and John L. Strother for their help and advice. I am especially indebted to William R. Anderson, Juliana Forneris, and Alicia Lourteig. Karin Douthit drew the handsome figures. I am grateful to the curators of the following herbaria for permitting me to study their specimens: A, AAU, BR, C, CAS, CM, CHAPA, DS, DUKE, ENCB, F, G, GH, GOET, JBSD, K, LE, LL, M, MEXU, MICH, MSC, MO, MT, NY, P, R, RB, S, SEL, TEX, U, UB, UPR, US, UTD, W, WIS. My study of *Stigmaphyllon* has been supported by a grant from the National Science Foundation to the University of Michigan (DEB-8215276).

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APPENDIX

Geographic listing of species of *Stigmaphyllon* by island(s) or country.

- Bahamas: *S. sagraeanum*.
 Cuba: *S. diversifolium*, *S. microphyllum*, *S. ovatum*, *S. sagraeanum*.
 Jamaica: *S. emarginatum*, *S. ovatum*, *S. puberum* (very rare).
 Hispaniola: *S. angulosum*, *S. emarginatum*, *S. laciniatum* (Gonâve Island), *S. ovatum*, *S. puberum*.
 Puerto Rico: *S. emarginatum*, *S. floribundum*, *S. ovatum*, *S. puberum*.
 Virgin Islands: *S. emarginatum*, *S. floribundum* (St. John, Virgin Gorda).
 Lesser Antilles: *S. adenodon* (Grenada), *S. ciliatum* (Barbados), *S. convolvulifolium* (Martinique, St. Vincent?), *S. diversifolium* (Anguilla to Martinique), *S. emarginatum* (Anguilla to Martinique except Dominica), *S. ovatum* (Guadeloupe, Martinique, St. Lucia), *S. puberum* (Guadeloupe, Martinique, Dominica, St. Vincent).
 Mexico: *S. ellipticum*, *S. lindenianum*, *S. ovatum*, *S. pseudopuberum*, *S. retusum*, *S. selerianum*.
 Guatemala: *S. ciliatum*, *S. cordatum*, *S. ellipticum*, *S. lindenianum*, *S. ovatum*, *S. pseudopuberum*, *S. puberum*, *S. retusum*.

Belize: *S. ciliatum*, *S. ellipticum*, *S. lindenianum*, *S. ovatum*, *S. puberum*, *S. retusum*.

El Salvador: *S. ellipticum*, *S. retusum*.

Honduras: *S. ciliatum*, *S. ellipticum*, *S. puberum*, *S. retusum*.

Nicaragua: *S. ciliatum*, *S. ellipticum*, *S. lindenianum*, *S. ovatum*, *S. puberum*, *S. retusum*.

Costa Rica: *S. adenophorum*, *S. columbicum*, *S. ellipticum*, *S. lindenianum*, *S. puberum*, *S. tonduzii*.

Panama: *S. ellipticum*, *S. humboldtianum*, *S. hypargyreum*, *S. lindenianum*, *S. ovatum*, *S. panamense*,
S. puberum.

TWO NEW SPECIES OF *STIGMAPHYLLON* (MALPIGHIACEAE) FROM SOUTH AMERICA

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Stigmaphyllon (Malpighiaceae) is a large genus of Neotropical, yellow-flowered vines with usually long-petioled, cordate leaves. In most species the stamens are heteromorphic, the styles bear apical flaps of tissue (the folioles for which the genus is named), and the samara has a large dorsal wing. The most recent treatment of the genus was published by Niedenzu in 1928, who saw rather little material, often in poor condition, from western and central South America. Recent collections, especially from Peru, include a number of new species, and also allow for a better understanding of variation in species already named and for their refined circumscription. Some older specimens, assigned various names, proved to be representatives of undescribed species. Two of these new species, one from Peru and one from Bolivia, are described here.

Stigmaphyllon tarapotense C. Anderson, sp. nov.—TYPE: PERU. San Martín: rd between Tarapoto and Juanjui, 21 km SE of Puente Colombia and 4.7 km SE of Juan Guerra, 30 Jun 1984, *Murray & Johnson 1530* (holotype: MICH).

Liana. Laminae 6.2–16 cm longae, 6.5–18 cm latae, ovatae vel reniformes vel orbiculares, supra glabrae, subtus dense argenteo-tomentosae, margine eglandulosae vel interdum glandulosae. Inflorescentia thyrsiformis constata ex umbellis, floribus in quaque umbella ca 15–30. Pedunculi 5.5–9.5 mm longi; pedicelli 5.5–9 mm longi. Bracteae 1.4–2.8 mm longae, triangulares; bracteolae 1.5–2.2 mm longae, triangulares, eglandulosae. Petala orbicularia; petala lateralia marginibus erosis, petalum posticum margine eroso-denticulato vel eroso-fimbriato. Stamina heteromorpha; antherae omnes fertiles, pubescentes. Stylus anticus 2.8–3.5 mm longus, apice 1.1–1.3 mm longo, lineari, unco ca 0.2 mm longo, foliolis absentibus; styli postici 3.7–4.7 mm longi, lyrati, apice 0.7–1.1 mm longo, foliolo variabili, 0.2–0.8 mm longo, 0.4–0.8 mm lato, parabolico vel oblongo vel ligulato, labio interdum tantum laterali. Samara ala dorsali 3.3–4.5 cm longa.

Vine. Stems and inflorescence axes densely sericeous, glabrate in age. Laminas 6.2–16 cm long, 6.5–18 cm wide, ovate to reniform or orbicular, apex mucronate, base cordate to subtruncate or in large leaves auriculate, glabrous above, densely silvery tomentose below, margin eglandular or occasionally with scattered sessile glands, basal glands prominent, sessile, each gland 1.8–3.2 mm in diameter; petioles 2–11.5 cm long; stipules triangular or broadly so, eglandular. Flowers ca 15–30 per umbel, these borne in thyrses. Peduncles 5.5–9.5 mm long, pedicels 5.5–9 mm long, terete, peduncles $\frac{2}{3}$ – $\frac{3}{4}$ times as long as or subequal or equal to pedicels; bracts 1.4–2.8 mm long, triangular or narrowly so, bracteoles 1.5–2.2 mm long, triangular, eglandular. Claw of anterior-lateral petals 1.8–2 mm long,

limb 10.5–11 mm long and wide, claw of posterior-lateral petals ca 1 mm long, limb ca 8.5 mm long and wide, all limbs orbicular, margin erose; claw of posterior petal 2.5–3 mm long, limb ca 7–8 mm long and wide, orbicular, margin erose-denticulate or erose-fimbriate, teeth and fimbriae up to 0.2 mm long. Stamens unequal, those opposite the posterior styles the largest, those opposite the anterior-lateral sepals (sometimes also those opposite the posterior-lateral sepals) with the connective enlarged and the locules somewhat reduced and unequal; anthers pubescent. Anterior style 2.8–3.5 mm long, shorter than the posterior two, glabrous or with a few scattered hairs near the base; apex 1.1–1.3 mm long including a spur ca 0.2 mm long, linear, folioles absent. Posterior styles 3.7–4.7 mm long, glabrous, lyrate; apex 0.7–1.1 mm long, folioles variable, 0.2–0.8 mm long, 0.4–0.8 mm wide, parabolic, oblong, or ligulate, or reduced to a narrow lip. Dorsal wing of samara 3.3–4.5 cm long, 1.5–2 cm wide; nut with 2–4 lateral winglets per side, usually in 2 rows; mature embryo not seen. Fig. 1.

ADDITIONAL SPECIMENS EXAMINED. PERU. San Martín: Dist. San Martín, valley of San Martín, 8 km E of Tarapoto, Fundo de San Isidro near Codo Creek, ca 1000 ft, 15 Aug 1937, *Belshaw* 3239 (F, GH, MICH, MO, NY, U, UTD, WIS); 6 km S of Tarapoto, on rd to Juanjui, 310 m, 18 Jul 1982, *Gentry et al.* 37688 (MICH, MO).

Stigmaphyllon tarapotense is known only from three collections from the vicinity of Tarapoto in Peru. It is notable for the very dense, silvery tomentose pubescence of the lower leaf surfaces. The posterior styles are unusual in that the folioles vary in size and shape in the same umbel and even in the same flower; sometimes the folioles are reduced to a lateral lip. The anterior style is efoliolate. The only other species in Peru with such densely pubescent, silvery leaves is *S. maynense* Huber, which may be readily distinguished by the structure of the androecium and gynoecium. In *S. maynense*, the posterior styles and their opposing stamens are shorter than the anterior style and its stamen; all styles are foliolate, and the anthers are glabrous. In *S. tarapotense*, as in most species, the posterior styles and associated stamens exceed the anterior ones; the anthers are pubescent. Also, the peduncles of *S. maynense* are very short (1–5 mm), while those of *S. tarapotense* are 5.5–9.5 mm long.

Stigmaphyllon yungasense C. Anderson, sp. nov.—TYPE: BOLIVIA. Depto La Paz, *Bang* 2296 (holotype: NY; isotypes: F, GH, MICH, MO, NY, W).

Liana. Laminae 10–15 cm longae, 7–11 cm latae, triangulares vel cordatae, supra glabrae, subtus tomentosae, margine eglandulosae. Inflorescentia dichasialis vel thyriformis constata ex umbellis vel umbella solitaria, floribus in quaque umbella ca (20–) 25–30. Pedunculi 8.5–18 mm longi; pedicelli 5.5–12 mm longi. Bracteae 1.6–2.5 mm longae, triangulares; bracteolae 1.4–1.9 mm longae, oblongae, eglandulosae. Petala orbicularia vel late obovata, marginibus fimbriatis. Stamina heteromorpha; antherae omnes fertiles, glabrae. Stylus anticus ca 3 mm longus, apice ca 1.3 mm longo, triangulari, obtuso, foliolis absentibus; styli postici ca 3 mm longi, apice ca 1.1 mm longo, unco ca 0.2 mm longo, foliolis absentibus. Samara ala dorsali ca 4.5 cm longa, ca 1.5 cm lata.

Vine. Stems and inflorescence axes with T-shaped hairs when young, glabrous in age. Laminas 10–15 cm long, 7–11 cm wide, triangular to cordate, apex mucronate, base cordate, glabrous above, tomentose below, margin eglandular, basal

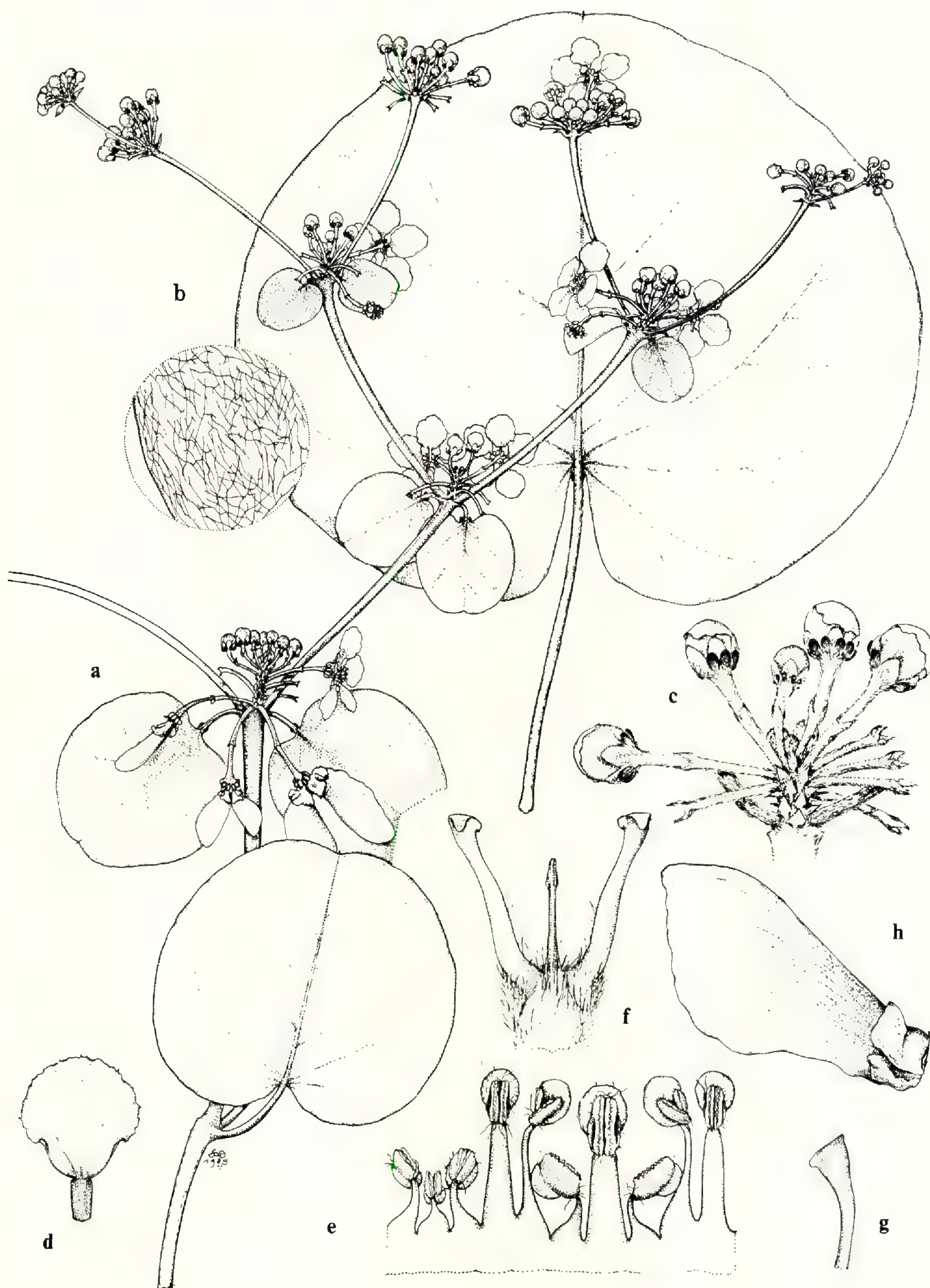


FIG. 1. *Stigmaphyllon tarapotense*. a. Flowering branch ($\times 0.5$). b. Large leaf ($\times 0.5$); detail of lower leaf surface ($\times 5$). c. Umbel ($\times 1.5$). d. Posterior petal ($\times 2$). e. Androecium ($\times 5$). f. Gynoecium ($\times 5$). g. Lateral view of anterior style ($\times 5$). h. Samara ($\times 1$). (Based on *Murray & Johnson 1530*).

glands prominent, sessile, each gland 1.5–2.1 mm in diameter; petioles 2.8–5.2 cm long; stipules triangular, eglandular. Flowers ca (20–) 25–30 per umbel, these borne in dichasia or small thyrses or solitary. Peduncles 8.5–18 mm long, pedicels 5.5–12 mm long, terete, peduncles 1–1.8 times as long as pedicels; bracts 1.6–2.5

mm long, triangular, bracteoles 1.4–1.9 mm long, oblong, eglandular. Claw of anterior-lateral petals ca 2 mm long, limb ca 11–11.5 mm long and wide, claw of posterior-lateral petals ca 1 mm long, limb ca 10 mm long and wide, claw of posterior petal ca 3 mm long, limb ca 8.5 mm long and wide, all limbs orbicular or broadly obovate, margin with fimbriae up to 0.5 (–0.6) mm long. Stamens unequal in size, those opposite the anterior-lateral sepals with the longest filaments; anthers all fertile, glabrous, none with the locules reduced. Anterior style ca 3 mm long, equal or subequal to the posterior two, glabrous; apex ca 1.3 mm long, triangular, obtuse, folioles absent. Posterior styles ca 3 mm long, glabrous, erect to recurved; apex ca 1.1 mm long including a spur ca 0.2 mm long, somewhat incurved, folioles absent. Dorsal wing of samara ca 4.5 cm long, ca 1.5 cm wide; nut with 1–3 lateral winglets per side; mature embryo not seen. Fig. 2.

ADDITIONAL SPECIMENS EXAMINED. BOLIVIA. Depto La Paz, Nor. Yungas, arriba de Puente Villa, Tarila Alto, 1850 m, bosque natural fragmentario en depresión de ladera, 8 Mar 1979 (sterile), *Beck 390* (MICH, MO), 22 Sep 1979 (flowers, young fruits), *Beck 2251 p.p.* (MICH).

This distinctive species is known only from three collections from the Yungas region of Bolivia. In most members of *Stigmaphyllon*, the posterior styles and their opposing stamens are larger than the anterior style and its opposing stamen; in a few species they are smaller. *Stigmaphyllon yungasense* is unusual in that its efoliolate styles are equal (or subequal) in size. The stoutest filaments with the largest anthers are those opposing the styles, but the stamens opposite the ante-



FIG. 2. *Stigmaphyllon yungasense*. a. Flowering branch ($\times 0.5$); detail of lower leaf surface ($\times 5$); single hair ($\times 10$). b. Posterior petal ($\times 2.5$). c. Androecium ($\times 5$). d. Gynoecium ($\times 5$); posterior style seen from above ($\times 10$). e. Samara ($\times 1$). (a–d based on *Bang 2296*; e based on *Beck 2251*.)

rior-lateral sepals have the longest filaments. The anthers are glabrous; none have the connective enlarged and the locules reduced or absent, a common condition in the stamens opposite the lateral sepals of other species. The only samaras seen were part of a mixed collection, *Beck 2251*. Of the two sheets at MICH, one consists of a few flowers and young to almost mature fruits of *S. yungasense*, the other of mature fruits of *Banisteriopsis muricata* (Cav.) Cuatr.

The earliest collection of *S. yungasense*, *Bang 2296*, was assigned to *S. bogotense* Tr. & Pl., an upland species of Colombia and adjacent Venezuela to central Peru but not recorded from Bolivia. *Stigmaphyllon bogotense* is similar in that its styles are efoliolate and subequal in size, none of its glabrous anthers consist of an enlarged connective and reduced locules, and the stamens opposite the anterior-lateral sepals often have the longest filaments. It differs in its leaves, which have a glandular margin, especially noticeable in young or small leaves, and in its inflorescences. The flowers (smaller than those of *S. yungasense*) are borne on pedicels that usually exceed the peduncles and are arranged most commonly in corymbs or pseudoracemes. Characteristically, the lowermost two flowers of an aggregate are separated on the axis a short distance from the others. The leaf margins of *S. yungasense* are eglandular. The pedicels are usually shorter than the peduncles, and the flowers are always borne in umbels (none is separated from the cluster).

Stigmaphyllon yungasense may also be confused with *S. florosum* C. Anderson, which does occur in the Yungas region. Its styles are also efoliolate, but the posterior ones have a narrow, lateral lip. The anthers are pubescent, and the stamens opposite the lateral sepals bear an enlarged connective and reduced locules. The leaf margins are beset with filiform glands and also with scattered sessile glands. *Stigmaphyllon florosum* has not been recorded above 1120 m.

ACKNOWLEDGMENTS

I thank the curators of the herbaria cited for the loans of specimens. Karin Douthit drew the illustrations. My study of *Stigmaphyllon* has been supported by a grant from the National Science Foundation to the University of Michigan (DEB-8215276).

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NOTES ON NEOTROPICAL MALPIGHIACEAE-II

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This paper treats thirty-two miscellaneous new species, new combinations, and already named but poorly known species that deserve new descriptions based on the collections now available. The genera and species are arranged alphabetically. For an explanation of the morphology of the Malpighiaceae and the terms I use to describe it, see my 1981 description of the Malpighiaceae of the Guayana Highland.

Aspicarpa brevipes (DC.) W. Anderson, comb. nov.

Banisteria brevipes DC., Prodr. 1: 591. 1824.

Gaudichaudia brevipes (DC.) Adr. Juss., Arch. Mus. Hist. Nat. 3: 597. 1843.

This is an earlier name for the plant generally called *Aspicarpa lanata* Rose. The type is a Sessé and Mociño plate, number 6331.951 in the Torner Collection of Sessé and Mociño Biological Illustrations at the Hunt Institute for Botanical Documentation. The drawing is very suggestive of *A. lanata*; especially noteworthy are the sometimes ternate leaves that are green above and whitish below due to the dense appressed vestiture, the short crowded axillary inflorescences, the circinate flower buds, and the five stamens and one style. On these bases alone I would be willing to apply the name to this species, but that conviction is greatly strengthened by study of a Sessé & Mociño specimen at G, ex herb. Barbey-Boissier. The specimen, which is definitely the species now called *A. lanata*, is a very close match for the Sessé and Mociño plate. After allowing for some modification by the artist and the loss of some open flowers when the specimen was pressed, I can hardly avoid the conclusion that the specimen at G should be considered a "typotype," i.e., the basis for a drawing that is a type. The species is common in the area of Guadalajara and west to near Tepic. It usually begins to flower in July, continuing until October or November. According to McVaugh (1972, p. 306), Sessé and Mociño reached Guadalajara early in April, 1791, stayed about four months, then traveled to Tepic near the end of July. They probably collected and drew this species in early July from around Guadalajara or in late July or early August from between Guadalajara and Tepic.

Another name that antedates Rose's 1903 name is *Banisteria virgata* Sessé & Mociño, Fl. Mex. 128. 1894?; ed. 2. 117. 1894. The description in the protologue fits this species very well; perhaps it was written to accompany the plate that DeCandolle named *Banisteria brevipes*. Sessé and Mociño described *B. virgata* from plants found blooming near Guadalajara in July, 1791.

Aspicarpa harleyi W. Anderson, sp. nov.

Fig. 1.

Suffrutex erectus 25–50 cm altus, ramis sericeis. Foliorum majorum lamina 2.6–6 cm longa, 1–2.5 cm lata, elliptica, basi cuneata vel rotundata, apice acuta, obtusa, vel raro rotundata, plerumque mucronata, supra velutina, subtus sericea



FIG. 1. *Aspicarpa harleyi*. a) habit, $\times 0.6$; b) leaf hairs, $\times 12$, upper from adaxial surface, lower from abaxial surface; c) node with axillary peduncles, $\times 3$; d) flower bud from above, anterior sepal lowermost, $\times$ ca 4; e) flower from above, posterior petal uppermost, $\times 3$; f) flower, side view, with sepals and petals removed to show androecium and gynoecium, claw of posterior petal to left, $\times 8$; g) intact fruit, oblique-anterior view, and above the anterior nutlet, side view, both $\times 3.5$. Drawn by Karin Douthit, a–c from *Harley 16823*, d–g from *Anderson 11758*.

vel subsericea, subtus prope basim utrinque (1–) 2 (–3) glandulas cylindricas ferens; petiolus 1.5–4 mm longus, laxe sericeus; stipulae 1.3–2 mm longae, subulatae. Flores omnes chasmogami, plerumque 1 in quaque axilla, pedunculo 2.5–6.5 mm longo, pedicello 4–10 mm longo. Sepala ovata, abaxialiter dense subsericea, adaxialiter appresso-tomentosa, per anthesin inter petala inflexa. Petala subaequalia, limbo brevifimbriato fimbriis plerumque glandulosis. Stamina fertilia 3, sepalis postico-lateralibus et antico opposita; antherae glabrae vel proximaliter in loculis tomentosae; staminodia 2, sepalis antico-lateralibus opposita, brevia, gracilia, glabra, per anthesin invisibilia. Nucula alula dorsali angusta dissecta instructa, sine alulis lateralibus, utrinque costata.

Subshrub 25–50 cm tall, much branched from the base, the stems erect, slender, woody but brittle, densely and persistently sericeous or belatedly glabrescent, the hairs very fine, appressed or somewhat spreading, originally stramineous or golden, fading to white in age; shoots springing in a clump from a short, knotty, swollen stock just below soil surface, also the source of relatively slender woody roots, with neither a vertically oriented turbinate tuber nor a laterally elongating and proliferating rhizome formed. Leaves decussate, bluish green above, silvery below; lamina of larger leaves 2.5–6 cm long, 1–2.5 cm wide, elliptical or slightly ovate, cuneate or rounded at base, entire at margin, acute, obtuse, or rarely rounded and usually mucronate at apex, bearing below on each side (1–) 2 (–3) cylindrical or slightly peltate glands 0.4–0.8 mm long, on veins just above base, very densely and persistently velutinous above with most hairs fine, white, V-shaped and 0.2–0.5 mm long but with an admixture (especially above midvein) of longer (1–2.5 mm) thicker yellow hairs that are sub-basifixed through suppression of 1 branch, very densely and persistently sericeous or subsericeous below with multiple layers of sessile or short-stalked, straight and appressed to somewhat sinuous and/or somewhat spreading hairs 0.4–3 mm long, the hairs between veins finer, shorter, white, those on veins thicker, longer, yellowish, the midrib and principal lateral veins [(4–) 5–6 (–7) on each side] flush or sunken above and very prominent below, the lateral veins strongly ascending and subparallel; petiole 1.5–4 (–8) mm long, loosely sericeous, eglandular; stipules 1.3–2 mm long, subulate, sericeous or distally glabrous, borne on stem beside petiole, persistent. Flowers all chasmogamous, borne in axils of full-sized leaves, mostly 1 per axil but occasionally 2 (–4) in a cluster, the floriferous peduncle or cluster of peduncles sessile or raised on an obscure stalk up to 2 mm long and subtended by several subulate or narrowly triangular bracts resembling stipules, 1.3–2.5 (–3.5) mm long; bracts and bracteoles abaxially loosely sericeous, adaxially sericeous to glabrous, eglandular, persistent; peduncle 2.5–6.5 mm long (–9 mm in fruit), loosely sericeous; bracteoles apical, subulate to narrowly elliptical, appressed or spreading, 1–2.1 mm long; pedicel 4–10 mm long (–16 mm in fruit), usually longer than peduncle, loosely sericeous. Flowers 15–19 mm in diameter, $\pm$ flat (i.e., all petals lying in 1 plane). Sepals quite distinct, 4–4.5 mm long, 2.3–3 mm wide, abaxially densely subsericeous, adaxially appressed-tomentose with fine white hairs except proximally in center, broadly ovate, acute at apex, valvate in bud, bent inward between petals in anthesis, the anterior eglandular and narrower, the lateral 4 biglandular, the glands green, yellow-green, dark red, or reddish purple, 1.2–1.7 mm long, 0.7–1 mm wide, separated and not compressed, attached nearly their whole length, free just at apex; sepals and glands enlarging somewhat as fruit matures and enclosing nutlets until maturity. Petals orange-yellow, glabrous or abaxially sparsely tomentose, the claw 2–3 mm long, the limb 5–6.5 mm long, 5.5–7 mm wide, flat, subcir-

cular, short-fimbriate all around margin except toward base with the fimbriae mostly tipped with tiny glands; posterior petal not or hardly different from lateral 4, its claw sometimes thicker, its limb more likely to be oblate. Fertile stamens 3, opposite anterior and posterior-lateral sepals; filaments 2–2.5 mm long, glabrous, distinct or connate just at base with adjacent filament or staminode; anthers 1–1.3 mm long, glabrous or finely tomentose proximally on locules, pressed against style in anthesis; staminodes 2, opposite anterior-lateral sepals, 1.5–2 mm long, straight or incurled at apex, hidden under sepals in anthesis, glabrous, slender, without remnant of anther or with a tiny globose apical swelling; minute nubbin of tissue with tuft of hairs present inside and between 2 posterior stamens, perhaps a rudiment of a sixth stamen. Ovary apparently glabrous, actually minutely puberulent, the 3 carpels free from each other, borne on a low common receptacle, the posterior 2 rotated so that all face the posterior petal; style 1, 3.3–3.6 mm long, glabrous, borne low on inner face of anterior carpel, the stigma capitate; stigma held above anthers or at the same level in anthesis. Fruit comprising 3 nutlets, or fewer through failure of 1 or 2 carpels to mature, all nutlets oriented toward posterior petal, minutely but very densely and persistently velutinous, the hairs very fine, white, basifixed, erect, 0.2–0.3 mm long; nutlet (in side view) 5.5–7.5 mm $\times$ 4.5–6 mm including a dorsal winglet 0.5–1.5 mm wide and proximally coarsely dissected into several obtuse or rounded teeth, the sides with prominent veins radiating from areole; lateral winglets absent, represented only by a rib along each side of nut, parallel to dorsal crest, continuous or not around base of nut, sometimes extruded into a few short knobs proximally; carpophore quite absent; ventral areole ovate, ca 2.5 mm $\times$ 2.5 mm, deeply concave and crescent-shaped in side view at maturity; torus after fall of nutlets only a low, rounded, inconspicuous mound. Chromosome number: $n = 40$ (counted in *Anderson 11758*).

TYPE: BRAZIL. Bahia: 26 km NW of Jacobina on road to Delfino (11°S, 40°17'W), 750 m, ridge with outcrop of blocky sandstone, abundant among rocks, 9 Mar 1976 fl/fr, *Anderson 11758* (MBM, holotype; CAS, CTES, F, G, K, M, MICH, NY, P, RB, SP, US, isotypes).

PARATYPES: BRAZIL. Bahia: Mpio Caitité, road from Caitité to Bom Jesus de Lapa, Km 22, cerrado, 1100 m, Apr fl/fr, *Carvalho et al. 1835* (MICH); Serra do Rio de Contas, 3 km N of Rio de Contas, 13°35'S, 41°50'W, 980 m, cut-over woodland by river, Jan fl/fr, *Harley 15351* (CEPEC, MICH); Serra do Curral Feio, 22 km NW of Lagoinha (which is 5.5 km SW of Delfino) on side road to Minas do Mimoso, 10°20'S, 41°20'W, 980 m, cerrado over sandstone rocks, Mar fl/fr, *Harley 16823* (CEPEC, MICH); Serra do Açuruá, ca 4 km N of São Inácio on road to Xique Xique, 11°05'S, 42°43'W, 500 m, cerrado on stony ground with shallow soils, Feb fl/fr, *Harley 19046* (MICH); Serra Geral de Caitité ca 5 km S of Caitité on road to Brejinhos das Ametistas, 14°07'S, 42°29'W, 1000 m, campos gerais, shrub- and herb-rich grassland with acaulous palms but few trees, Apr fl/fr, *Harley 21145* (MICH).

I am happy to name this interesting species for R. M. Harley, who first collected it and has found it repeatedly since. The species, which is endemic to Bahia, is disjunct from its relatives, a group of species found between 20°S and 35°S. That group includes *A. pulchella* (Griseb.) O'Don. & Lourt. [called *A. sericea* (St.-Hil.) Nied. by Niedenzu], *A. salicifolia* (Chodat) Nied., *A. schininii* W. Anderson [called *A. lanata* (Chodat) Nied. by Niedenzu], and *A. sericea* Griseb. [called *A. argentea* (Griseb.) Nied. by Niedenzu]. None of those species has vesture like that of *A. harleyi*, although there is a superficial similarity between the leaves of *A. harleyi* and those of the Paraguayan endemic *A. schininii*.

Among other differences, *A. schininii* is notable for having broader, subcordate leaves, cleistogamous flowers, chasmogamous flowers borne mostly in pairs raised on a well-developed common stalk, anthers with an apical tuft of hairs, long curved staminodes with an enlarged hairy apex, and a chromosome number of $n=20$ (counted in *Anderson 11777*).

Aspicarpa schininii W. Anderson, nom. nov.

Camarea lanata Chodat, Arch. Sci. Phys. Nat., sér. 3, 24: 499. 1890; Mém. Soc. Phys. Genève 31, pt. 2, n. 3: 20, fig. 49. 1892.

Aspicarpa lanata (Chodat) Nied., Verz. Vorles. Königl. Akad. Braunschweig Winter-Semester 1912/13: 59. 1912, non *Aspicarpa lanata* Rose, Contr. U.S. Natl. Herb. 8: 49. 1903.

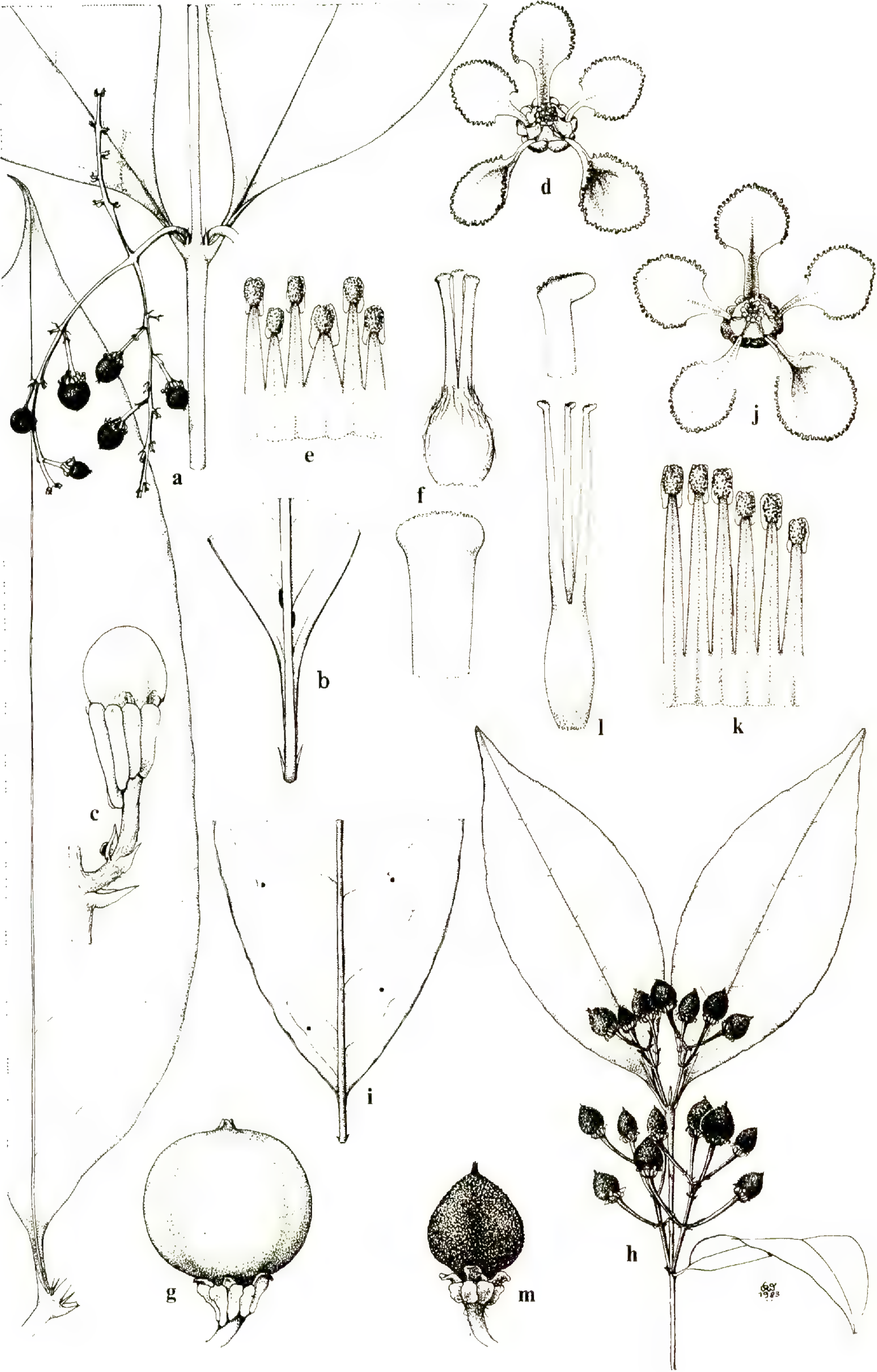
Gaudichaudia lanata (Chodat) Chodat, Bull. Soc. Bot. Genève, sér. 2, 9: 101. 1917.

It is a pleasure to name this wholly Paraguayan species in honor of an excellent Paraguayan botanist, Aurelio Schinini. I shall treat it in detail in my monograph of *Aspicarpa*. See notes above under *A. harleyi*.

Bunchosia acuminata Dobson, Syst. Bot. 8: 275. 1983.

Fig. 2, a–g.

Shrub 1–2.5 m tall; stems initially very sparsely sericeous but soon glabrous, initially flattened, becoming terete in age. Lamina of larger leaves 16–28 cm long, 4–10 cm wide, narrowly to broadly elliptical, cuneate at base, acuminate at apex with the acumen 4–22 mm long, initially bearing scattered appressed hairs but glabrous at maturity, bearing 1 gland below on each side near base or up to 15 mm above it and beside midrib or between midrib and margin, the fine reticulum usually prominulous above; petiole 10–15 (–19) mm long, soon glabrate; stipules 1.2–3.5 mm long. Inflorescences axillary or terminal, simple or ternate, when ternate the lateral branches axillary to much-reduced biglandular leaves (“bracts”), sericeous to glabrate, the individual branches 3–12 cm long and containing 4–22 flowers, these mostly decussate; bracts 1.5–3 mm long, narrowly triangular or ovate, often acuminate; peduncle rarely lacking, usually 0.7–3 mm long; bracteoles 1–1.7 mm long, ovate, 1 of the pair (occasionally both) bearing 1 (rarely 2) raised eccentric basal-abaxial glands 0.5–1 mm in diameter; pedicel 3–7.5 mm long, sericeous to glabrate. Sepals extending 0.2–1 mm beyond glands, obtuse or rounded, glabrous or ciliate on margin; glands 8, 1.5–3.5 mm long, the anterior 2 shortest and the posterior 2 longest, elliptical, compressed, glabrous, detached at apex, the posterior 2 decurrent with about $\frac{1}{2}$ their length on pedicel. Petals light yellow, glabrous, the outermost with the limb concave and glandular-erose or bearing very small glands on margin, the other 4 $\pm$ flat and bearing sessile or short-stalked glands all around margin; lateral petals with the claw 1–2 mm long, the limb 4–5.5 mm long, 4–6 mm wide; posterior petal with the thick claw 3 mm long, the limb 3.5–4 mm in diameter. Filaments 2.3–2.5 mm long opposite sepals, 1.5–1.8 mm long opposite petals, glabrous, ca $\frac{1}{3}$ – $\frac{1}{2}$ connate; anthers 0.8–1.1 mm long, glabrous, pressed against styles, the connectives light brown and somewhat glandular-swollen at apex. Gynoecium 3-carpellate; ovary ca 1.5 mm high, globose, 3-locular, loosely sericeous on distal $\frac{1}{2}$; styles 3, $\frac{2}{3}$ connate or coherent to quite distinct, 1.7–2 mm long, glabrous, held erect and together at or just above level of anthers; stigmas capitate. Fruit orange to red at maturity, 10–13 mm long and 15–16 mm in diameter (dried), oblate, 3-lobed, glabrous, smooth.



SPECIMENS STUDIED. BRAZIL. Bahia: Mpio Itambé, Sapucaia, basin of Rio Pardo, Nov fl, *Fróes* 12660/26 (NY, holotype); Mpio Prado, 45 km N of Alcobaça, wet forest, 25–75 m, Mar fr, *Mori et al.* 9728 (MICH); Mpio Maraú, Km 15 on Ubaitaba/Maraú road, disturbed wet forest, Feb imm fl, *Mori et al.* 11342 (MICH); Uruçuca-Taboquinha highway, forest, Apr fr, *Pinheiro* 1242 (CEPEC, MICH); Uruçuca/Ilheus, cacao plantation, Jul fr, *Pinheiro* 1498 (CEPEC, MICH); 16 km from Itapé at Faz. Santa Helena on Rio Colonia, Oct fl, *Pinheiro* 2025 (CEPEC, MICH); Km 25 on Guaratinga/São Paulinho highway, forest, Apr fl, *Pinheiro* 2083 (CEPEC, MICH); Uruçuca/Banco do Pedro, forest, Apr fr, *Santos* 664 (CEPEC, MICH); Mpio Ilhéus, area of CEPEC, Sep fr, *Santos* 3661 (MICH).

This species and *B. macilenta* were described by Dobson, without illustration, on the basis of few and incomplete specimens. I provide here expanded descriptions of both, the only tricarpetate species in Bahia, with an illustration that shows comparable structures. The following couplet will aid in distinguishing between them.

1. Stems soon glabrous; lamina of larger leaves 16–28 cm long, 4–10 cm wide; leaf glands 2; inflorescence simple or ternate; filaments 1.5–2.5 mm long, alternately long (opposite sepals) and short (opposite petals); ovary sericeous on distal ½; styles 1.7–2 mm long; fruit 10–13 mm long, 15–16 mm in diameter (dried), smooth. *B. acuminata.*
1. Stems persistently hairy, eventually glabrate; lamina of larger leaves 7–13 cm long, 2.5–5.1 cm wide; leaf glands usually 4; inflorescence simple; filaments 3–4 mm long, the anterior 5 long, the posterior 5 short; ovary glabrous; styles 4 mm long; fruit 7–9 mm long, 7–8 mm in diameter (dried), granulate. *B. macilenta.*

***Bunchosia berlinii* W. Anderson, sp. nov.**

Fig. 3.

Frutex vel arbor parva 2–3 m alta. Foliorum majorum lamina 26–43 cm longa, 11–15.5 cm lata, elliptica, apice acuminata, abaxialiter dense et pertinaciter argenteo-sericea; petiolus 12–20 mm longus; stipulae 2.5–3.5 mm longae. Inflorescentia 7–20 cm longa, simplex et sine foliis, sericea, floribus 30–90, congestis, ca 4–5 per cm; bracteae 4–6 mm longae; pedunculus plerumque nullus; bracteolae 1.5–2.5 mm longae, 1 bracteola cujusque paris 1 glandula abaxiali excentrica 1–1.5 mm diametro instructa. Sepala abaxialiter sericea, glandulis 8, 3–4.7 mm longis. Petalum extimum limbo concavo, eroso vel proximaliter fimbriato; cetera 4 petala limbo ± plano, toto circuitu fimbriato, aliquot fimbriis ut videtur glandulosis. Antherarum connectivum pallide brunneum. Gynoecium 3-carpellatum, glabrum; stylus 1 (ex 3 stylis omnino connatis), stigmatе trilobo. Fructus aurantiacus vel ruber, siccus 12–15 mm longus et diametro, glaber, granulatus.

Shrub or small tree 2–3 m tall; stems sericeous to glabrate. Lamina of larger leaves 26–43 cm long, 11–15.5 cm wide, elliptical, cuneate at base, abruptly acuminate at apex with the acumen 15–35 mm long, bearing 1 large gland on each side of midrib below at base and distally an inframarginal row of 6–10 small glands, soon glabrate above, densely and persistently silvery-sericeous below, completely covered by 2 layers of straight sessile hairs, the outer layer of stouter, longer hairs 1–1.5 mm long; petiole 12–20 mm long, sericeous; stipules 2.5–3.5 mm long. Inflorescence 7–20 cm long, without leaves and unbranched, sericeous, the flowers 30–90 or more, crowded, mostly 4–5 or more per cm, borne in no

FIG. 2. *Bunchosia acuminata* and *B. macilenta*. a–g, *B. acuminata*: a) node with infructescence, and separate leaf, ×0.5; b) base of leaf and stipules, abaxial side, ×1; c) flower bud, posterior calyx glands to left, ×3.5; d) flower from above, oblique view, posterior petal uppermost, ×2; e) partial androecium, laid out, abaxial view, the stamen at right opposite posterior petal, ×7; f) gynoecium, ×7, with apex of 1 style below, ×30; g) fruit, ×1.5. h–m, *B. macilenta*: h) fruiting branch, ×0.5; i) base of leaf and stipules, abaxial side, ×1; j) flower from above, oblique view, posterior petal uppermost, ×2; k) partial androecium, laid out, abaxial view, the stamen at right opposite posterior petal, ×7; l) gynoecium, ×7, with apex of 1 style above, ×30; m) fruit, ×1.5. Drawn by Karin Douthit, a from *Pinheiro* 1242, b and g from *Pinheiro* 1498, c–f from *Pinheiro* 2083, h, i, m from *Santos* 2389, j–l from *Pinheiro* 1757.

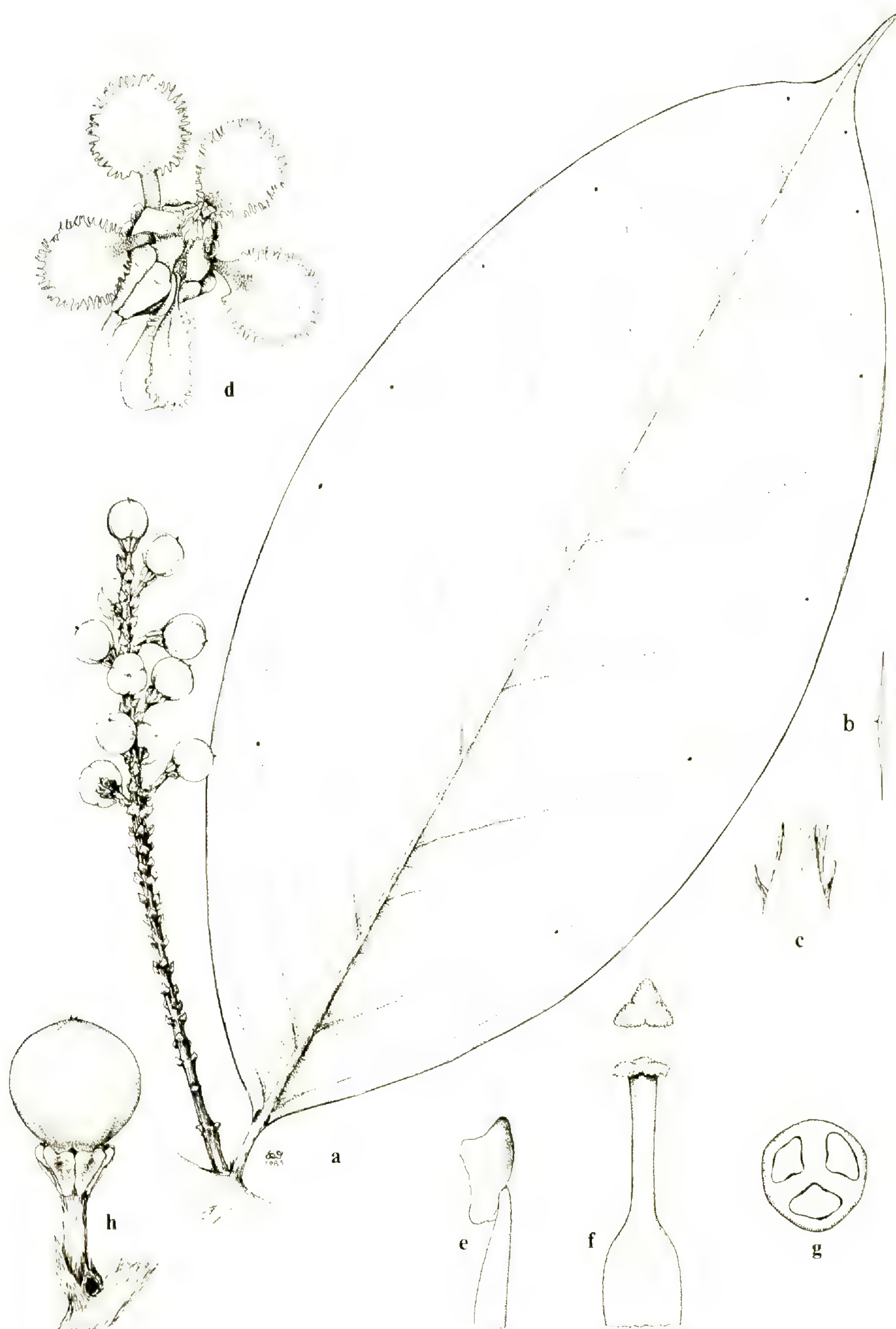


FIG. 3. *Bunchosia berlinii*. a) leaf (abaxial side) and inflorescence, $\times 0.5$; b) hair from abaxial surface of lamina, $\times 15$; c) stipules on base of petiole, $\times 2.5$; d) flower, posterior petal uppermost, $\times 2.5$; e) stamen, side view, $\times 10$; f) gynoecium, $\times 10$, with separate view of stigma from above; g) cross section of ovary, $\times 15$; h) fruit, $\times 1.5$. Drawn by Karin Douthit, a-c and h from *Berlin 1777*, d-g from *Berlin 856*.

regular arrangement; bracts 4–6 mm long, narrowly triangular; peduncle mostly none, rarely up to 1 mm long; bracteoles 1.5–2.5 mm long, triangular, 1 of the pair bearing 1 large eccentric abaxial gland 1–1.5 mm in diameter; pedicel 4.5–7.5 mm long in flower, up to 9 mm and thickened in fruit, sericeous. Sepals extending 0.5–1.5 mm beyond glands, rounded, abaxially sericeous, ciliate on margin, adaxially glabrous, pressed inward against filaments; glands 8, 3–4.7 mm long, obtriangular, compressed, decurrent with about $\frac{1}{2}$ their length on pedicel, marginally and adaxially pilose, slightly recurved at apex. Petals light yellow except pigmented (red?) in claw and base of limb, glabrous, the outermost with the limb deeply concave and erose or proximally fimbriate, the other 4 $\pm$ flat, all fimbriate all around margin, the fimbriae sometimes somewhat glandular, especially proximally on posterior petal; lateral petals with the claw 2.5–3.5 mm long, the limb 5–5.5 mm long, 4.5–7 mm wide; posterior petal with the claw 3–3.5 mm long, bearing 2 short projections at apex, the limb 4–5 mm in diameter. Filaments 2.2–2.5 mm long, longer opposite sepals than petals, ca $\frac{1}{2}$ connate, those opposite petals sometimes with an apical tuft of hairs; anthers 0.8–1.5 mm long, longer and with more pendulous locules opposite sepals than petals, glabrous, pressed against styles, the connectives light brown and somewhat glandular-swollen at apex. Gynoecium 3-carpellate, glabrous; ovary ca 1.5 mm high, globose, 3-loculed; style 1 (formed from 3 completely connate), ca 2 mm long, the stigma large, 3-lobed, the 3 stigmas nearly distinct. Fruit orange to red, 12–15 mm long and in diameter (dried), globose or ovoid, glabrous, granulate.

TYPE: PERU. Amazonas: Ca 10 km N of Quebrada Huampami, primary forest, 180–240 m, 24 Jul 1974 fr, *Berlin 1777* (MICH, holotype; MO, isotype).

PARATYPES: PERU. Amazonas: all from vicinity of Huampami, Río Cenepa, 4°30'S, ca 78°30'W, 180–330 m: Apr imm fr, *Ancuash 249* (MO); 5 km E of Chávez Valdía, primary forest, Jul fr, *Ancuash 1110* (MICH); primary forest, *Ancuash 1291* (MO); abandoned chacra, Sep fr, *Berlin 117* (MICH, MO); old secondary forest, Feb fl, *Berlin 856* (MICH, MO); Quebrada Shimpunts, primary forest, Feb fl/imm fr, *Berlin 879* (MO); primary forest, S of Río Cenepa, Jul fr, *Berlin 1663* (MICH, MO); primary forest, Jul fr, *Berlin 1839* (MICH, MO); secondary forest, Aug fr, *Berlin 2006* (MO); Quebrada Chigkishinuk, Jan fl, *Kayap 289* (MO), Apr fl/imm fr, *626* (MO); Jul fr, *Kayap 1049* (MO), *1193* (MICH, MO); Aug fr, *Kayap 1472* (MICH, MO); 5 km E of Chávez Valdía, *Kujikat 14* (MICH), Aug fr, *Kujikat 276* (MICH, MO).

Very few species of *Bunchosia* have densely silvery-sericeous leaves, and among those the only one previously described from Amazonia is *B. argentea* (Jacq.) DC., a bicarpellate species with smaller leaves, shorter inflorescences containing fewer flowers, dentate petals, a sericeous ovary, and free styles. The relationships of *B. berlinii* probably lie elsewhere, perhaps with the large-leaved tricarpetate species most diverse in Central America, such as *B. lanieri* Watson and *B. macrophylla* Rose. From that difficult group, none of which occurs in Amazonia, *B. berlinii* is amply distinguished by its large sericeous leaves, long many-flowered inflorescences, large bracts and bracteoles, sessile pedicels, and glabrous ovary.

This species is named in honor of Brent Berlin, an anthropologist who collected it repeatedly between September, 1972, and August, 1975.

Bunchosia bonplandiana Adr. Juss., Ann. Sci. Nat. 2° Sér. Bot. 13: 324. 1840; Arch. Mus. Hist. Nat. 3: 332. 1843. Fig. 4.

Jussieu based this name on a specimen without locality data found in Bonpland's American herbarium. I have not seen the type, which could not be found when I worked at P in 1981, but there is a photograph at MICH (F negative 35566). That photograph and Jussieu's description combine to show that Bonpland's specimen had an unusual combination of characters: gynoecium 3-carpellate, glabrous,



FIG. 4. *Bunchosia bonplandiana*. a) flowering branch, $\times 0.5$; b) flower bud and portion of inflorescence, $\times 2.5$; c) flower, side view, $\times 5$; d) posterior petal, adaxial side, $\times 5$; e) stamen, abaxial side, $\times 10$; f) gynoecium, $\times 10$; g) cross section of ovary, $\times 15$. Drawn by Karin Douthit from *Hutchison & Wright 4032*.

with the styles free; leaves nearly glabrous, biglandular near the base; inflorescence leafless, unbranched, short, and few-flowered; sepals glabrous except for the ciliate margin. To that description Dobson (1976), who studied the type, added that the petals were eglandular-erose and the calyx glands were 7–8, not 10 as stated by Jussieu. Dobson thought the species must exist, but he did not find any specimens that match the above description in the course of his work. I have encountered one such collection. It is *Hutchison & Wright 4032*, collected 5 February 1964 in flower in Peru, Amazonas, Bongara, along the road to La Rioja, 3 km N of north end of Lago Pomacocha, rich ceja forest with many epiphytes, 2100–2200 m (MICH). The locality is noteworthy for two reasons: 1) It is unusually high for Malpighiaceae, and that kind of forest is an unusual habitat for the family; 2) Humboldt and Bonpland passed near that area in August, 1802, as they travelled from Huanca-bamba to Cajamarca (Sandwith 1926), when they could have collected the type. *Hutchison & Wright 4032* is not a perfect match for the type of *B. bonplandiana*. Its leaves are only about half as large, and at least one of every pair of bracteoles bears well-developed glands, whereas Jussieu said the bracteoles were only “glandular-thickened at base” and Dobson called them eglandular. However, the similarity is great enough to make me unwilling to describe 4032 as a new species at this time. It is described in full below, as a start toward an expanded concept of *B. bonplandiana* and as a contribution toward our record of the flora of Peru; Macbride (1950) did not treat any specimens that could be this species. If *Hutchison & Wright 4032* is really *B. bonplandiana*, future collections should fill in the range between the small leaves described here and the larger leaves of the type. The description below is based only on *Hutchison & Wright 4032*.

Shrub 2.5 m tall; stems initially sericeous but immediately glabrescent. Lamina of larger leaves 5.8–7.2 cm long, 2.2–2.7 cm wide, elliptical, cuneate at base, acute or acuminate at apex, bearing 1 fairly large gland on each side of

midrib below near base, between midrib and margin, glabrous at maturity, the reticulum prominulous on both sides; petiole 5–8 mm long, sparsely sericeous to glabrate; stipules ca 1 mm long. Inflorescence 2.5–5 cm long, without leaves and unbranched, single in axils of current leaves, very sparsely sericeous to glabrate, the flowers 6–10, distant; bracts 1–1.4 mm long, triangular; peduncle 3–5 mm long; bracteoles ca 1 mm long, broadly triangular, 1 or more often both of each pair bearing 1–2 abaxial glands, the second gland smaller when present; pedicel 6.5–9.5 mm long, sparsely sericeous to glabrate. Sepals extending 1–1.4 mm beyond glands, rounded, glabrous except for the ciliate margin; glands 8 (or 7 due to partial to complete fusion of 2), 1.8–2.3 mm long, elliptical or obovate, compressed, not or only slightly decurrent, glabrous. Petals “clear bright yellow,” glabrous, the outermost deeply concave, the other 4 shallowly concave; lateral petals with the claw 2 mm long, the limb 4 mm long, 3–5 mm wide, erose, eglandular; posterior petal spatulate, the thick claw 2.5–2.8 mm long, the limb 3.8–4 mm long, 1.8–2 mm wide, erose, the margin glandular-thickened in proximal $\frac{1}{2}$. Filaments 2.4–3 mm long, longer opposite sepals than petals, ca $\frac{1}{3}$ connate; anthers 0.7–1 mm long, glabrous, the connectives yellow or light brown and not notably glandular-swollen. Gynoecium 3-carpellate, glabrous; ovary ca 1.5 mm high, 3-loculed; styles 3, quite distinct, ca 1.5 mm long, lengthening in age. Fruit unknown.

Bunchosia macilenta Dobson, Syst. Bot. 8: 274. 1983.

Fig. 2, h–m.

Shrub 1–1.5 m tall; stems subvelutinous or subsericeous to eventually glabrate, slightly flattened or terete. Lamina of larger leaves 7–13 cm long, 2.5–5.1 cm wide, elliptical, cuneate or decurrent at base, acuminate at apex with the acumen 5–15 (–20) mm long, thinly sericeous to glabrate, the hairs longer persistent below than above, bearing usually 2 glands below on each side between midrib and margin in proximal $\frac{1}{3}$ – $\frac{1}{2}$, the fine reticulum often prominulous on both sides; petiole 6–10 mm long, sericeous to glabrate; stipules 0.5–1.5 mm long. Inflorescences 0.7–2.5 cm long, axillary, without leaves and unbranched, loosely sericeous, the flowers 4–8, decussate; bracts 1.3–2.2 mm long, triangular; peduncle 2–3 mm long (–6 mm in fruit); bracteoles 0.8–1.5 mm long, triangular or ovate, eglandular or 1 or both bearing 1 or 2 small glandular areas abaxially on margin, these never raised or well-defined glands; pedicel 6–13 mm long, thinly sericeous to glabrate. Sepals extending 1–1.6 mm beyond glands, broadly obtuse or rounded, abaxially sparsely sericeous, ciliate on margin, adaxially glabrous; glands 8, 1.3–2.2 mm long, obovate or orbicular, slightly compressed, glabrous, detached just at apex, the posterior 2 slightly decurrent. Petals light yellow, glabrous, glandular-laciniate all around limb or entire at base; outermost petal with the claw 2.5–3 mm long, the limb deeply concave, 4.5–5.5 mm long, 6–7 mm wide; other lateral petals with the claw 2–3 mm long, the limb flat, 3.5–4 mm long, 3–4 mm wide; posterior petal with the thick claw 3.5 mm long, the limb 4 mm long, 4.5–5 mm wide. Filaments 3–4 mm long, the anterior 5 longer than the posterior 5, the 1 opposite posterior petal shortest of all, glabrous, up to $\frac{1}{3}$ connate, erect or somewhat spreading; anthers 0.7–1 mm long, glabrous, the connectives yellow or pale brown and slightly swollen. Gynoecium 3-carpellate; ovary 1.5 mm high, ovoid, 3-locular, glabrous; styles 3, distinct except connate just at base, 4 mm long, glabrous, very slender, erect or divergent distally, held well above anthers (ca 1 mm); stigmas obliquely capitate with a short abaxial extension. Fruit color at maturity not known, 7–9 mm long and 7–8 mm in diameter (dried), ovoid, glabrous, granulate.

SPECIMENS STUDIED. BRAZIL. Bahia: *Blanchet 1512* (F, P, isotypes); Mpio Sta. Cruz de Cabrália, 4–6 km E of Estação Ecológica do Pau-brasil (ca 17 km W of Porto Seguro), wet forest, Aug fl, *Mori et al. 10793* (MICH); Alcobaça branch toward S. Antonio, thicket, Jan fl, *Pinheiro 1757* (CEPEC, MICH); Km 36 on highway from Teixeira de Freitas to Itamaraju, forest, Aug fr, *Santos 2389* (CEPEC, MICH).

See discussion under *Bunchosia acuminata*.

***Bunchosia plowmanii* W. Anderson, sp. nov.**

Fig. 5.

Frutex vel arbor parva 1.5–4 m alta. Foliorum majorum lamina 7–14 cm longa, 3.5–6.5 cm lata, abaxialiter pertinaciter sericea vel subvelutina et glandulis et basalibus et distalibus instructa. Inflorescentia 3–10 cm longa, simplex et sine foliis, floribus (4–) 8–26; 1 bracteola 1 glandula abaxiali excentrica 0.5–1 mm diametro instructa. Petala limbo eglanduloso vel irregulariter eroso-glanduloso vel toto circuitu glanduloso. Antherarum connectivum flavidum vel pallide brunneum. Gynoecium 2 (–3)-carpellatum, glabrum vel sparsim sericeum; styli 2 (–3), liberi vel proximaliter cohaerentes. Fructus aurantiacus vel ruber, siccus 5–8 mm longus, 4.5–8 mm diametro, glaber vel glabratus, granulatus.

Shrub or small tree 1.5–4 m tall; stems sericeous or subvelutinous to soon glabrate. Lamina of larger leaves 7–14 cm long, 3.5–6.5 cm wide, elliptical or slightly obovate, cuneate at base, mostly abruptly short-acuminate at apex, initially sericeous but very soon glabrous above, persistently sericeous or subvelutinous below with the hairs varying from dense to sparse and appressed to some-

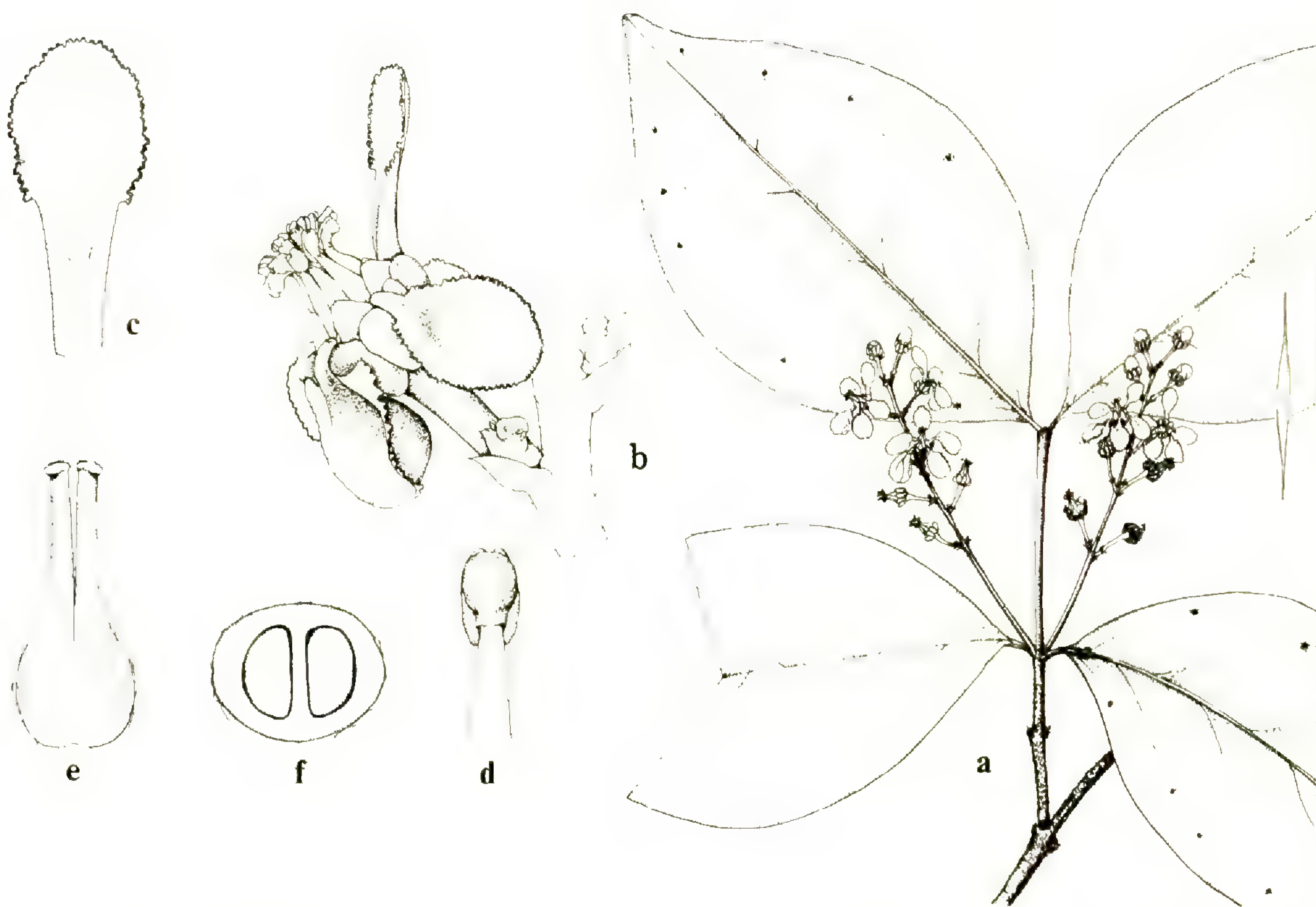


FIG. 5. *Bunchosia plowmanii*. a) flowering branch, $\times 0.5$, with hair from abaxial surface of lamina, $\times 25$; b) flower, side view, $\times 2.5$; c) posterior petal, adaxial side, $\times 3.5$; d) stamen, abaxial side, $\times 7.5$; e) gynoecium, $\times 7.5$; f) ovary, cross section, $\times 10$. Drawn by Karin Douthit from the type.

what raised, bearing below 1 gland near base on each side of midrib and distally 1–10 or more in an inframarginal row, the apex with a small gland, the reticulum often prominulous on both sides; petiole 5–9 mm long, sericeous or subvelutinous to glabrate; stipules 0.5–0.8 mm long. Inflorescences 3–10 cm long, axillary and rarely terminal, without leaves and unbranched, sericeous or subvelutinous to glabrate, the flowers (4–) 8–26, mostly decussate but occasionally inserted irregularly; bracts 1–2.8 mm long, ovate or triangular; peduncle 0.5–3 mm long; bracteoles ca 1 mm long, ovate, 1 of each pair bearing 1 prominent eccentric abaxial gland 0.5–1 mm in diameter; pedicel 4–8 mm long (–11 mm in fruit), usually muricate. Sepals extending 1–2 mm beyond glands, rounded, glabrous except ciliate on margin; glands 8, 1.7–2.7 mm long, obovate, mostly compressed, glabrous, attached their whole length or detached at apex, not or hardly decurrent. Petals light yellow, glabrous, all glandular-dentate all around limb or the glands few or none, the glands (if present) increasing in size and number from outermost petal to innermost (posterior) petal; lateral petals recurved, posterior erect; outermost petal with the claw 3–3.5 mm long, the limb 5 mm long, 6 mm wide, deeply concave; other 3 lateral petals with the claw 2–2.5 mm long, the limb 4–6 mm long, 3–4.5 mm wide, shallowly concave to flat, roughly rectangular; posterior petal spatulate, the thick claw 3.5–4 mm long, the limb 4 mm long, 3.5 mm wide. Filaments 2.5–3.3 mm long, longer opposite sepals than petals, glabrous, ca $\frac{1}{3}$ – $\frac{1}{2}$ connate; anthers 0.8–1.3 mm long, glabrous, pressed against styles and reflexed, the connective yellow or light brown and glandular-swollen. Gynoecium 2 (–3)-carpellate; ovary 1.5 mm high, 2 (–3)-locular, glabrous or sparsely sericeous; styles 2 (–3), distinct or weakly coherent in proximal $\frac{1}{3}$ – $\frac{1}{2}$, 2–2.2 mm long, glabrous or sparsely sericeous, held erect and together at or just above level of anthers; stigmas capitate. Fruit orange to red at maturity, 5–8 mm long and 4.5–8 mm in diameter (dried), ovoid or globose, glabrous or glabrate, granulate.

TYPE: PERU. Tumbes: Prov. Contralmirante Villar, Huasimo, Quebrada Ucumares, 550 m, thicket along road, 12 Feb 1976 fl, *Plowman 5442* (MICH, holotype; F, isotype).

PARATYPES: ECUADOR. Guayas: Guayaquil, inner edge of mangrove thicket, Feb fl, *Asplund 15305* (S), Mar fr, *Asplund 15638* (S); Cerro Azul, near Chongon, 130 m, Mar fr, *Dodson et al. 9650* (MICH, MO). El Oro: dry disturbed tropical forest SW of Arenillas, 80 m, Apr/May fr, *Escobar 1340* (MICH, QCA, SEL), fl, *Escobar 1349* (MICH, QCA). Loja: Celica-Zapotillo Road, 5–6 km S of Sabanilla, disturbed deciduous forest, 600 m, Apr fl, *Harling & Andersson 18277* (GB, MICH); Sabiango Hill, 1400 m, Nov fl, *Townsend A.119* (US).—PERU. Tumbes: Prov. Zarumilla, below El Caucho, open thicket in dry tropical forest, 350–450 m, Feb fr, *Plowman 5479* (MICH), fl, *Plowman 5480* (MICH). Lambayeque: Prov. Lambayeque, Km 28 E of Olmos, 1150–1200 m, Jan fr, *Hutchison & Wright 3437* (F, MICH).

I am happy to dedicate this species to Timothy Plowman, an excellent field botanist who not only made three good collections of it in 1976, but even had the foresight to pickle flowers for the specialist. *Bunchosia plowmanii* is endemic to dry tropical forests on the Pacific slopes of southwestern Ecuador and adjacent Peru. The species is distinguished by its dry habitat, hairy leaves bearing distal as well as basal glands, few-flowered pseudoracemes, light-colored anther connectives, usually bicarpellate and glabrous or only sparsely sericeous gynoecium, distinct styles, and small fruits. The only collection seen with tricarpellate gynoecia is *Escobar 1340*, and in that the tricarpellate flowers are exceptions on shoots with most flowers bicarpellate.

Gaudichaudia chasei W. Anderson, sp. nov.

Fig. 7, h-o.

Planta volubilis, caulibus vestustioribus lignosis. Foliorum majorum lamina 5–8 cm longa, 2.4–3.8 cm lata, basi cuneata vel truncata, apice acuta vel obtusa, utrinque sparsim sericea; petiolus 4–9 mm longus. Flores omnes chasmogami, in umbellis 4-floris portati, umbellis in dichasiis foliosis; bracteae bracteolaeque 3–5.5 mm longae, 1–2.5 mm latae; pedunculus (6–) 8–11 (–14) mm longus; pedicellus 4–5 (–6) mm longus. Sepala apice late rotundata, glandulis 1–1.4 mm longis. Petala dentata; 4 lateralibus ungue 1.2–2 mm longo, limbo 4.5–6 mm longo, 4–6 mm lato; posticum ungue 2–3 mm longo, limbo 4–5.5 mm longo, 4.5–6 mm lato. Stamina 5, omnia fertilia; filamenta 1.5–1.8 mm longa, plerumque libera vel basi brevissime connata; antherae 0.6–0.9 mm longae, basi apiceque rotundatae. Styli 3, aequales, 1.2–2 mm longi. Samara obcordata, 12–14 mm longa, 10–12 mm lata; ala lateralis basi attenuata, acuta vel acuminata, apice incisa; ala dorsalis 0.5–2 mm lata; alulae intermediae utrinque 1–3.

Vine with the stems sericeous to glabrate, becoming woody with punctiform lenticels in age. Leaves strictly decussate, smaller on flowering lateral shoots than on main stems; lamina of larger leaves 5–8 cm long, 2.4–3.8 cm wide, ovate or elliptical, cuneate to truncate at base, usually bearing on each side somewhat above base 1 (–2) marginal toothlike or filamentous projections up to 1 mm long, acute or obtuse at apex, thinly but persistently sericeous on both sides or eventually glabrescent, the hairs sessile, straight, appressed, the midrib and principal lateral veins (3–5 on each side) raised below; petiole 4–9 mm long, sericeous to glabrate; stipules up to 0.5 mm long, triangular, borne on stem beside petiole. Flowers all chasmogamous, borne in 4-flowered umbels arrayed in leafy dichasia, loosely sericeous; peduncle (6–) 8–11 (–14) mm long; bracts and bracteoles 3–5.5 mm long, 1–2.5 mm wide, mostly elliptical, abaxially sparsely sericeous, adaxially glabrous, eglandular, $\pm$ spreading, the bracts deciduous in fruit, the bracteoles apical, bent together toward 1 side, persistent; pedicel 4–5 (–6) mm long, always shorter than peduncle, usually ca $\frac{1}{2}$ as long, straight in bud. Flowers 13–17 mm in diameter, flat (i.e., all petals lying in 1 plane) or the lateral petals more strongly reflexed than the posterior. Sepals 2–2.8 mm long, 1.5–2.2 mm wide, abaxially sericeous in center, otherwise glabrous except for ciliolate margin, green except for hyaline margin, broadly rounded at apex, appressed in anthesis, the anterior eglandular, the lateral 4 biglandular, the glands green, 1–1.4 mm long, 0.6–0.8 mm wide, compressed or slightly separated, free just at apex. Petals orange-yellow, the outermost usually with a red spot in center, glabrous, the limb flat, subcircular or broadly elliptical, dentate and eglandular all around margin, the cutting coarser on posterior petal; lateral 4 petals with the claw 1.2–2 mm long, the limb 4.5–6 mm long, 4–6 mm wide; posterior petal with the claw 2–3 mm long, the limb 4–5.5 mm long, 4.5–6 mm wide. Stamens 5, opposite sepals, all fertile, glabrous; filaments 1.5–1.8 mm long, broad, mostly free or connate only at base; anthers 0.6–0.9 mm long, often reflexed in anthesis, rounded at base and apex, about as wide at apex as at base, the narrowly elliptical or triangular connective dark red. Ovary densely hispid; styles 3, all alike, 1.2–2 mm long, shorter than stamens or exceeding them slightly, glabrous, straight and erect or divergent, constricted below the small slightly capitate terminal stigma; gynoecium (judged from the styles) apparently rotated slightly so that no carpel lies on plane of symmetry passing through anterior sepal and posterior petal. Samara thinly sericeous, obcordate, 12–14 mm long, 10–12 mm wide, the lateral wing tapered to an acute or acuminate base and notched at apex $\frac{1}{2}$ – $\frac{3}{4}$ of the distance to the nut, sometimes somewhat sinuous, flat or somewhat wavy;

carpophore 6 mm long; dorsal wing 0.5–2 mm wide, irregularly lobed; intermediate winglets 1–3 on each side, similar in size and shape to dorsal wing, mostly oriented parallel to lateral wing; small ventral winglet present between apex of nut and notch in lateral wing. Chromosome number: $n = 40$ (counted in *Anderson 12945*).

TYPE: MEXICO. Morelos: 6 km SE of Cuernavaca on Hwy 138 to Yautepec, Cañón de Lobos, with limestone walls and outcropping on hillsides, 1300 m, 2 Oct 1983 fl/fr, *Anderson 12945* (MICH, holotype; BM, CAS, CHAPA, DUKE, ENCB, F, G, GH, IBUG, K, M, MEXU, MO, NY, P, TEX, UC, US, W, isotypes).

PARATYPE: MEXICO: Morelos: Cañón de Lobos, 20 km al ESE de Cuernavaca, bosque tropical deciduo en la ladera sur del cañón, 1350 m, Aug fl, *Flores Crespo 18 p.p.* (MEXU; the sheet at ENCB is a different species of *Gaudichaudia*).

Gaudichaudia chasei is named for Mark W. Chase, keen student of the Orchidaceae. We visited the Cañón de Lobos at Dr. Chase's insistence, in search of *Leochilus*. We found this new species instead of the orchid, so it seems only fair to name it for Chase.

Among the diploid species without cleistogamous flowers, this one is probably closest to *G. mcvaughii* W. Anderson; see below in this paper for a comparison of the two. It also seems to be closely related to *G. cynanchoides* H. B. K., a widespread weedy species which differs in having less woody stems, more or less V-shaped leaf hairs, at least above, many cleistogamous flowers that develop early and set many fruits, shorter bracts and bracteoles, 1–2 (–3) styles in the chasmogamous flowers, and a smaller subcircular samara that is entire or just emarginate at the apex and lacks winglets between the lateral wing and the very low dorsal wing or rib. Preliminary study suggests that a tetraploid entity ($n = 80$) common in Puebla and Oaxaca may have originated through hybridization between *G. cynanchoides* and *G. chasei*.

***Gaudichaudia cycloptera* (DC.) W. Anderson, comb. nov.**

Hiraea? cycloptera DC., Prodr. 1: 586. 1824.

This is apparently the oldest name for the species that Niedenzu (1928) called *Gaudichaudia pentandra* Adr. Juss.

***Gaudichaudia krusei* W. Anderson, sp. nov.**

Fig. 6.

Suffrutex 0.3–1.2 m altus, ramis sericeis vel subsericeis. Foliorum majorum lamina 3.5–9 cm longa, 1–4 cm lata, ovata vel elliptica, basi rotundata vel subcordata, apice acuta vel abrupte breviacuminata, supra sericea, subtus sericea, subsericea, vel appresso-tomentosa; petiolus 2–6 mm longus. Flores omnes chasmogami, in umbellis 4-floris portati; bractee bracteolaeque 2–3.5 mm longae, 0.7–1.5 mm latae; pedunculus 1–5 mm longus; pedicellus 3–11 mm longus. Petala lateralia ungue 1.3–1.7 mm longo, limbo 4.5–6.5 mm longo latoque; posticum ungue 2.5–3 mm longo, limbo 4.5–5.5 mm longo, 5–6 mm lato. Stamina 5, omnia fertilia; antherae 1–1.5 mm longae, cordiformes. Styli 3, aequales, 2–3.3 mm longi. Samara circularis vel obcordata, 6.5–11 mm diametro; ala lateralis basi rotundata vel acuta, apice incisa; ala dorsalis 0.5–1.5 mm lata, dentata; alulae intermediae utrinque 2–7.

Shrub 0.3–1.2 m tall, with few to many slender erect non-twining stems from a woody underground base, the stems $\pm$ persistently sericeous or subsericeous. Leaves opposite or occasionally (on same plant) in 3s; lamina of larger leaves 3.5–9

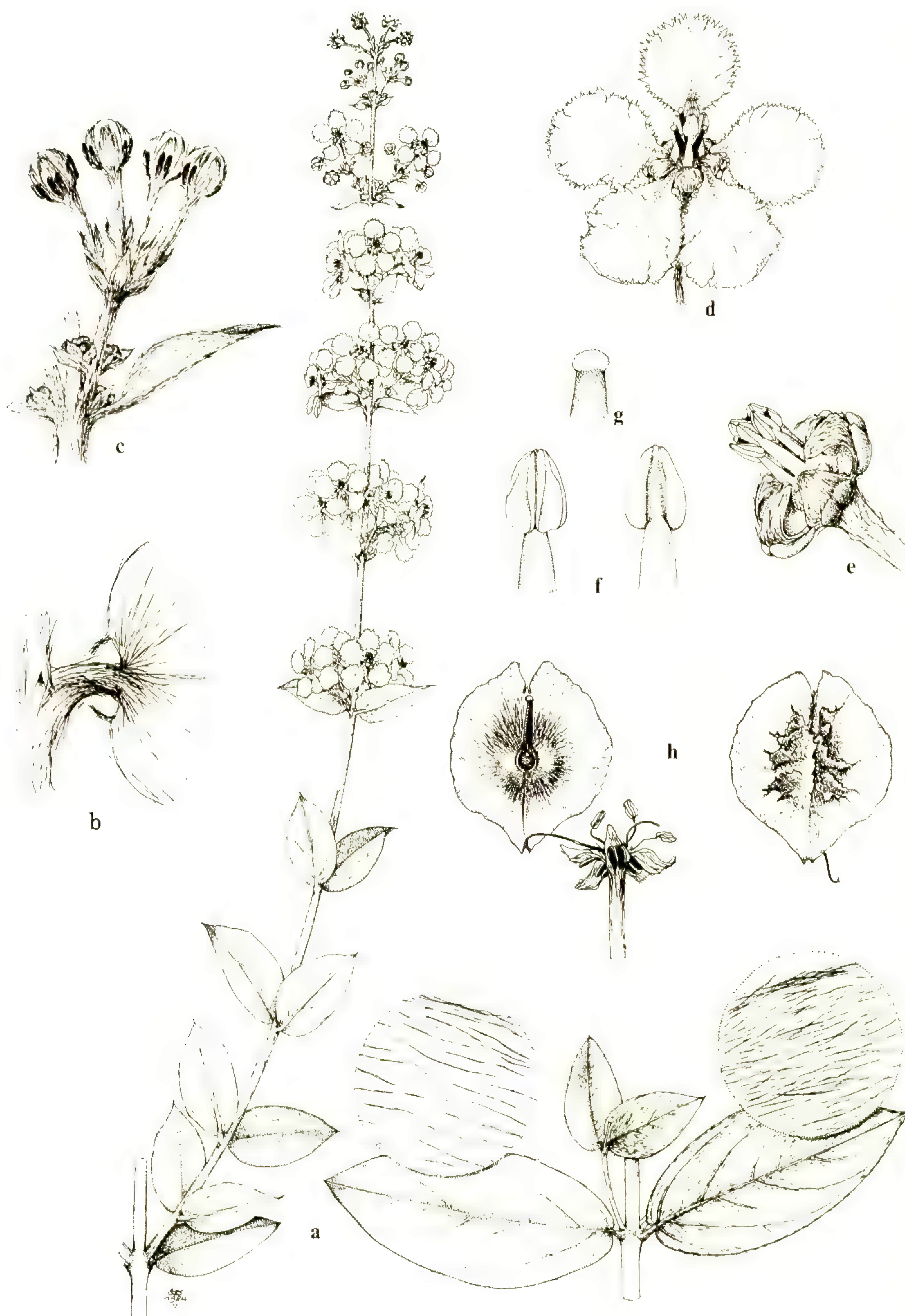


FIG. 6. *Gaudichaudia krusei*. a) flowering branch and large leaves, $\times 0.5$, with enlargements of adaxial surface of lamina (left) and abaxial surface (right), $\times 5$; b) base of leaf, $\times 5$; c) umbel in bud, $\times 2.5$; d) flower, oblique-anterior view, $\times 2.5$; e) flower with petals removed, side view, $\times 4$; f) anthers, adaxial side left, abaxial side right, $\times 10$; g) stigma, $\times 25$; h) samaras, adaxial side left, still attached by carpophore to receptacle, abaxial side right, $\times 2.5$. Drawn by Karin Douthit, a–g from *Anderson 12868*, h from *Koch & Fryxell 8264*.

cm long, 1–4 cm wide, ovate or narrowly ovate to elliptical, rounded or subcordate at base and usually bearing a marginal filamentous process up to 1 (–1.5) mm long on each side of petiole, acute to abruptly short-acuminate at apex, sericeous above with sessile, $\pm$ straight, parallel hairs, sericeous, subsericeous, or appressed-tomentose below with the long, fine, sessile or short-stalked hairs varying from straight and appressed to somewhat sinuous or spreading, the hairs usually much denser below than above, the midrib and principal lateral veins (3–5 on each side) prominent below; petiole 2–6 mm long, sericeous to velutinous; stipules up to 1 mm long, triangular, borne on stem beside petiole. Flowers all chasmogamous, borne in 4-flowered umbels arrayed in short crowded dichasia of 1, 3, or occasionally more umbels in the axils of distally gradually smaller leaves; inflorescences loosely sericeous or appressed-tomentose; bracts and bracteoles eglandular, abaxially loosely subsericeous, adaxially glabrous, appressed or spreading, the bracts 2–3.5 mm long, 0.8–1.5 mm wide, narrowly ovate-triangular, the bracteoles 2–3 mm long, 0.7–1 mm wide, narrowly elliptical; peduncle 1–5 mm long; pedicel 3–11 mm long, usually longer than peduncle, straight in bud. Flowers 14–18 mm in diameter, $\pm$ flat (i.e., all petals lying in 1 plane). Sepals 2.4–3.5 mm long, 1.5–2 mm wide, abaxially sericeous except for a hyaline marginal band, ciliolate or denticulate on margin, adaxially glabrous, obtuse or rounded at apex, incurved between petals and inrolled at apex in anthesis, the anterior eglandular, the lateral 4 biglandular, the glands green, 1.2–1.7 mm long, 0.5–0.7 mm wide, compressed in middle of sepal, attached their whole length or free just at apex. Petals orange-yellow, glabrous, the limb flat, subcircular, irregularly dentate to short-laciniate, the cutting coarser on posterior petal, eglandular or some divisions slightly glandular, especially proximally; lateral 4 petals with the claw 1.3–1.7 mm long, the limb 4.5–6.5 mm long and wide; posterior petal with the claw 2.5–3 mm long, the limb 4.5–5.5 mm long, 5–6 mm wide. Stamens 5, opposite sepals, all fertile, glabrous; filaments 1.7–3 mm long, distinct or the posterior 2 up to $\frac{1}{3}$ connate; anthers 1–1.5 mm long, cordiform in outline, subcordate at base, obtuse at apex, the narrowly triangular connective dark red to black in dried specimens. Ovary densely hispid; styles 3, all alike, 2–3.3 mm long, shorter than stamens or exceeding them slightly, glabrous or rarely sparsely sericeous, straight and erect or more commonly divergent, constricted below the capitate terminal stigma; gynoecium (judged from the styles) apparently rotated slightly so that no carpel lies on plane of symmetry passing through anterior sepal and posterior petal. Samara loosely sericeous to glabrate on wing, subcircular to obcordate, 6.5–11 mm in diameter, the lateral wing rounded to acute at base and notched at apex ca $\frac{1}{2}$ of the distance to the nut, often somewhat sinuous and denticulate, somewhat convex as viewed dorsally; carpophore 4–5 mm long; dorsal wing 0.5–1.5 mm wide, dentate; intermediate winglets 2–7 on each side, as high as width of dorsal wing, mostly at right angles to lateral and dorsal wings; samaras separating from a short pyramidal torus. Chromosome number: $n = 40$ (counted in *Anderson 12868*).

TYPE: MEXICO. Guerrero: Microondas road up Cerro Alquitrán, marked “El Tejocote” on Hwy 95 W of Mazatlán, ca 6.5 km from Hwy 95, with oaks, scattered pines, open brushy understory, 1600 m, 29 Sep 1983 fl/imm fr, *Anderson 12868* (MICH, holotype; CAS, CHAPA, DUKE, ENCB, G, K, MEXU, MO, NY, isotypes).

PARATYPES: MEXICO. Guerrero: Near type locality, red clay soil, 1750 m, Jul sterile, *Anderson & Anderson 4979* (ENCB, MICH); Hwy 95, Km 39–40, ca 5 km N of El Rincón, dry slopes and rocky

ravine through sparse oak forest, ca 1500 m, Jan fl, *Croat 45687* (MO); Rincón Viejo [NW of Rincón de la Via], "laderas con bosque de encino, con suelos de arcilla arenosa con pH 6, en sombra parcial o pleno sol, entre Gramíneas," 750 m, Aug fl, Oct fr, *Kruse 82* (ENCB, Kruse Herb.), Sep fl, *Kruse 1289* (Kruse Herb.); 1 km N of Rincón de la Via, 725 m, Aug fl, *Kruse 1288*, Oct fr, *Kruse 1290* (both Kruse Herb.); Cerro "El Peregrino," "a todo lo largo del filo plano del parte aguas y unicamente dentro de una distancia de dos a tres metros del filo," 530–810 m, Aug fl, *Kruse 1920 & 1921* (Kruse Herb., not seen, MICH!, photo); 40 km S of Chilpancingo, granitic soil on mountainside beside swift stream, mixed pine and cacti, Aug fl, *Paxson et al. 17M788* (F, MEXU, NY, US); Mpio Mochitlán, 38 km S of Chilpancingo, transition from oak zone to tropical forest, clay soil, 880 m, Oct fl/fr, *Koch et al. 79137* (MICH); Mpio Acapulco, 3 km W of Cuarenta y Dos, which is 27 km N of Acapulco on road to microwave station "42 y La Providencia," grassy savannah, soil of granitic sand, 610 m, Oct fl/imm fr, *Koch et al. 79220* (ENCB, MEXU, MICH); Mpio Chilpancingo, 22 km S of Chilpancingo, 1150 m, Oct fl/fr, *Koch & Fryxell 8264* (MICH); ca 3 km S of Acahuizotla, pine-oak forest, 1050 m, Jul fl, *Rowell 3094* (MICH); Mpio Chilpancingo, E slope of Cerro Alquitrán, near Mazatlán, "ladera caliza con vegetación de bosque abierto de *Quercus*, *Pinus* y *Bursera*," 1500 m, Jul fl, *Rzedowski 22681* (ENCB); Cerro "Del Alquitrán," beyond Petaquillas, SE of Chilpancingo, 1400 m, 22 Oct 1978 fl, *Schwabe et al. s.n.* (MEXU). Without state: *Haenke* [1402] (F), [1528] (F, NY), both collected in 1791.

I am naming this very distinctive species in honor of Hubert Kruse, an enthusiastic student of the flora of Guerrero, through whose collections and friendly assistance I first learned about it and its narrow distribution in the hills south and west of Chilpancingo. *Gaudichaudia krusei* is probably most closely related to *G. subverticillata* Rose, another shrubby species, endemic to Jalisco and southern Nayarit. *Gaudichaudia subverticillata* has at least the lower stem hairs long-spreading; the leaves, often in verticils of three, are larger and more loosely hairy on both sides, and lack marginal processes at the base; the inflorescence is more elaborately compound, with the umbels not displayed in simple axillary dichasia; the petals are elliptical, notably longer than wide; and the samara is larger and entire or only slightly emarginate at the apex, and lacks intermediate winglets.

***Gaudichaudia mcvaughii* W. Anderson, sp. nov.**

Fig. 7, a–g.

Planta volubilis, caulibus vetustioribus lignosis. Foliorum majorum lamina 3–8.5 cm longa, 1.8–4 cm lata, basi cordata vel brevihastata, apice plerumque rotundata vel obtusa; petiolus 1–4 mm longus. Flores omnes chasmogami, in umbellis 4-floris portati, umbellis plerumque 1 vel 3 in quaque inflorescentia axillari; bracteae (1–) 1.5–3 mm longae, 0.8–1.2 mm latae; pedunculus 3–10 mm longus; bracteolae 1.3–2.6 mm longae, 0.7–1.4 mm latae; pedicellus 4–14 mm longus. Sepala apice late rotundata, glandulis 2–3 mm longis. Petala dentata vel brevifimbriata; 4 lateralia ungue 1.5–2 mm longo, limbo (6–) 7–9.5 mm longo, (6–) 7–10 mm lato; posticum ungue 3–4 mm longo, limbo (5–) 6–7 mm longo, 6–8.5 mm lato. Stamina 5, omnia fertilia; filamenta 1.5–2.5 mm longa, plerumque $\frac{1}{4}$ – $\frac{3}{4}$ connata; antherae 1.2–2 mm longae, triangulares vel cordiformes. Styli 3, aequales, 2–2.8 mm longi. Samara $\pm$ circularis, 10–18 mm diametro; ala lateralis basi rotundata vel parum emarginata, apice incisa, non plana; ala dorsalis 1.5–3 (–6) mm lata; alulae intermediae utrinque (0–) 3–5.

Vine with the young stems strongly twining, densely velutinous, tomentose, or subsericeous to soon or eventually glabrate, becoming woody with small punctiform lenticels in age. Leaves strictly decussate; lamina of larger leaves 3–8.5 cm long, 1.8–4 cm wide, ovate or elliptical, cordate or short-hastate at base with the lobes rounded or triangular and often bearing 1–2 (–3) filamentous processes 0.2–0.5 (–1) mm long, mostly rounded or obtuse and often mucronate at apex but sometimes acute, initially thinly velutinous above with V-shaped hairs, these persis-



FIG. 7. *Gaudichaudia mcvaughii* and *G. chasei*. a–g, *G. mcvaughii*: a) habit and large leaf, $\times 0.5$, with enlargements of adaxial surface of lamina (left) and abaxial surface (right), $\times 5$; b) flower bud in umbel, $\times 2.5$; c) flower, oblique-anterior view, $\times 2$; d) flower with petals removed, side view, $\times 5$; e) anthers, abaxial side left, adaxial side above, $\times 7.5$; f) stigma, $\times 30$; g) samara, abaxial side, $\times 1.5$. h–o, *G. chasei*: h) habit, $\times 0.5$, with enlargements of adaxial surface of lamina (left) and abaxial surface (right), $\times 5$; i) base of leaf, $\times 1$; j) flower bud in umbel, $\times 2.5$; k) flower, from above, posterior petal in middle, $\times 2$; l) flower with petals removed, side view, $\times 5$; m) anthers, abaxial side below, adaxial side above, $\times 7.5$; n) stigma, $\times 30$; o) samaras, adaxial side left, still attached by carpophore to receptacle, abaxial side right, $\times 1.5$. Drawn by Karin Douthit from the types.

tent or deciduous, usually more densely and persistently velutinous to tomentose to sericeous below, the hairs extremely variable in shape and density between populations, within populations, and even on the same plant, the midrib and principal lateral veins (4–6 on each side) prominent below; petiole 1–4 mm long, often shorter than basal lobes of lamina, velutinous; stipules very small (0.2–0.5 mm long), triangular, borne on stem beside petiole. Flowers all chasmogamous, borne in short-stalked 4-flowered umbels, the inflorescence a short axillary shoot comprising 1 umbel or 3, velutinous to subsericeous; bracts and bracteoles abaxially sparsely sericeous, adaxially glabrous, usually bearing a glandular marginal spot on each side near base, the bracts (1–) 1.5–3 mm long, 0.8–1.2 mm wide, ovate-triangular, the bracteoles 1.3–2.6 mm long, 0.7–1.4 mm wide, elliptical, apical, $\pm$ spreading; peduncle 3–10 mm long; pedicel 4–14 mm long, at least slightly longer than peduncle, straight in bud. Flowers 16–24 mm in diameter, $\pm$ flat (i.e., all petals lying in 1 plane). Sepals 3–4.5 mm long, 2–2.7 mm wide, sparsely sericeous abaxially in center, otherwise glabrous except for the ciliolate margin, green in the center, membranous and hyaline toward margin, broadly rounded at apex, the lateral 4 or all 5 incurved between petals in anthesis, the anterior eglandular, the lateral 4 biglandular, the glands green, 2–3 mm long, 0.5–1 mm wide, compressed in middle of sepal, attached their whole length. Petals orange-yellow, glabrous, the limb flat, subcircular, dentate or short-fimbriate and eglandular all around margin, the divisions slightly deeper on posterior petal; lateral 4 petals with the claw 1.5–2 mm long, the limb (6–) 7–9.5 mm long, (6–) 7–10 mm wide; posterior petal with the claw 3–4 mm long, the limb (5–) 6–7 mm long, 6–8.5 mm wide. Stamens 5, opposite sepals, all fertile, glabrous; filaments 1.5–2.5 mm long, broad, mostly connate for $\frac{1}{4}$ – $\frac{3}{4}$ of their length; anthers 1.4–2 mm long, triangular or cordiform in outline, subcordate at base and acute or obtuse at apex, the narrowly triangular connective dark red to black in dried specimens. Ovary densely hispid; styles 3, all alike, 2–2.8 mm long, shorter than stamens, glabrous, straight and erect or divergent, constricted below the slightly capitate terminal stigma; gynoecium (judged from the styles) apparently rotated slightly so that no carpel lies on plane of symmetry passing through anterior sepal and posterior petal. Samara loosely sericeous, roughly circular, 10–18 mm in diameter, the lateral wing usually rounded or slightly emarginate at base and notched or incised at apex up to $\frac{2}{3}$ of the distance to the nut, irregularly somewhat sinuous, moderately to strongly wavy (i.e., the wing not lying in 1 plane); carpophore 4–5 mm long; dorsal wing 1.5–3 (–6) mm wide; intermediate winglets (0–) 3–5 on each side, as high as width of dorsal wing or often much shorter, mostly at right angles to lateral and dorsal wings, somewhat confluent with the lateral wing. Chromosome number: $n = 40$ (counted in *Anderson 12699*).

TYPE: MEXICO. Colima: 11 km SSW of Colima on Hwy 110, limestone hill with very dense cover of shrubs and small trees, 390 m, 18 Sep 1983 fl/fr, *Anderson 12699* (MICH, holotype; CAS, DUKE, ENCB, F, G, IBUG, K, MEXU, MO, NY, P, US, isotypes).

PARATYPES: MEXICO. Jalisco, Mpio La Huerta, Estación de Biología Chamela: Vareda Chachalaca, selva baja caducifolia, Oct fr, *Lott 692* (MEXU, MICH), Oct fl, *Magallanes 3868* (MICH), Nov fr, *Magallanes 3935* (MEXU), Oct fl, *Cervantes S. 18* (MICH). Colima: 8 km SSW of Colima on Hwy 110, brushy roadside near thorn-scrub on limestone, 390 m, Sep fl/fr, *Anderson 12703* (CAS, ENCB, MEXU, MICH, MO, NY); Microondas La Cumbre, ca 8 km SE of Colima on Hwy 110, limestone hill with brushy cover, 400–500 m, Sep fl/fr, *Anderson 12708* (CAS, DUKE, IBUG, MEXU, MICH, NY); road to Playa del Oro, ca 1.6 km S of Hwy 110 W of Santiago, limestone hills above the coast, 120 m, Sep fl/fr, *Anderson 12713* (BM, CAS, CHAPA, ENCB, F, MEXU, MICH, NY, TEX);

mountain summits near pass ca 18 km SSW of Colima on Manzanillo road, deciduous woodland now nearly in full foliage, 500 m, Aug fl, *McVaugh 16043* (CAS, DUKE, MEXU, MICH, NY); road from Hwy 15 to Playa del Oro (W of Santiago), ca 1.8 km from beach, dense low forest on steep slopes, Sep fl, *Stevens 1884* (CAS, ENCB, MICH, MO). Guerrero: Mpio Tecpan, torre de microondas cerca de Papanoa, cerro de caliza con bosque tropical caducifolia, 380 m, Oct fl/fr, *Koch & Fryxell 82218* (MICH); rocky headland in front of Hotel Mirador, Acalpulco, ca 100 m, Aug fl/fr, *MacDaniels 143* (F); Acapulco and vicinity, Oct fl/fr, *Palmer 8* in 1895 (F, GH, MEXU, MO, NY, US). Without state, *Haenke* [1401] in 1791 (F).

Gaudichaudia mcvaughii is named for my mentor, colleague, and friend, Rogers McVaugh. It is a species of the low deciduous woodland found on limestone between sea level and 500 m in the Pacific lowlands from Jalisco to Guerrero, a distribution which it shares with many other species, including *Malpighia ovata* Rose. Exploration of suitable habitats in Michoacán should lead to its eventual collection in that state.

Gaudichaudia mcvaughii seems to be rather isolated among the diploid species without cleistogamous flowers. In its short axillary inflorescences and in many details of the flowers and fruits it resembles *G. subverticillata* Rose and *G. krusei* W. Anderson, but both of those species are non-twining shrubs or subshrubs. Among the vining species the one most like *G. mcvaughii* in its flowers and fruits is *G. chasei*. The following couplet summarizes the most easily observed differences between the two species.

1. Petiole 1–4 mm long; lamina cordate or short-hastate at base, thinly velutinous to glabrescent above; bracts up to 3 mm long, bracteoles to 2.6 mm; pedicel longer than the peduncle; flowers 16–24 mm in diameter; calyx glands 2–3 mm long; filaments mostly connate for $\frac{1}{4}$ – $\frac{3}{4}$ of their length; anthers 1.4–2 mm long; samara rounded or emarginate at base. *G. mcvaughii*.
1. Petiole 4–9 mm long; lamina cuneate to rounded at base, thinly sericeous to glabrescent above; bracts and bracteoles 3–5.5 mm long; pedicel shorter than peduncle, usually ca $\frac{1}{2}$ as long; flowers 13–17 mm in diameter; calyx glands 1–1.4 mm long; filaments mostly free or connate only at base; anthers 0.6–0.9 mm long; samara tapered to an acute or acuminate base. *G. chasei*.

Heteropterys alata (W. Anderson) W. Anderson, comb. nov.

Heteropterys beecheyana Adr. Juss. var. *alata* W. Anderson, Mem. N.Y. Bot. Gard. 32: 184. 1981.

Further consideration of this taxon has led me to the conclusion that it deserves species status as much as several other species generally recognized in the pink-flowered complex of *Heteropterys*.

Heteropterys aliciae W. Anderson, sp. nov.

Fig. 8.

Planta volubilis ramis velutinis mox vel demum glabratis. Foliorum majorum lamina 4.5–7 cm longa, 2–3.8 cm lata, subtus margine biglandulosa et pertinaciter velutina vel subsericea; stipulae epipetiolares. Flores in pseudoracemis 0.8–3 cm longis portati; pedunculus 2.5–3.5 mm longus; bracteolae eglandulosae, plerumque inter medium et apicem pedunculi portatae; pedicellus 2.3–3 mm longus. Sepala appressa per anthesin. Petala flava, abaxialiter laevia. Styli apice truncati vel apiculati. Samara 23–33 mm longa; nux laevis.

Vine with slender woody stems, climbing to 2 m; stems velutinous to glabrate and soon developing raised punctiform lenticels, the hairs V-shaped with each branch 0.1–0.3 mm long. Lamina of larger leaves 4.5–7 cm long, 2–3.8 cm wide, elliptical or slightly ovate, obtuse, rounded, or subcordate at base, acute to rounded and often mucronate at apex, bearing 1 gland below on each side on

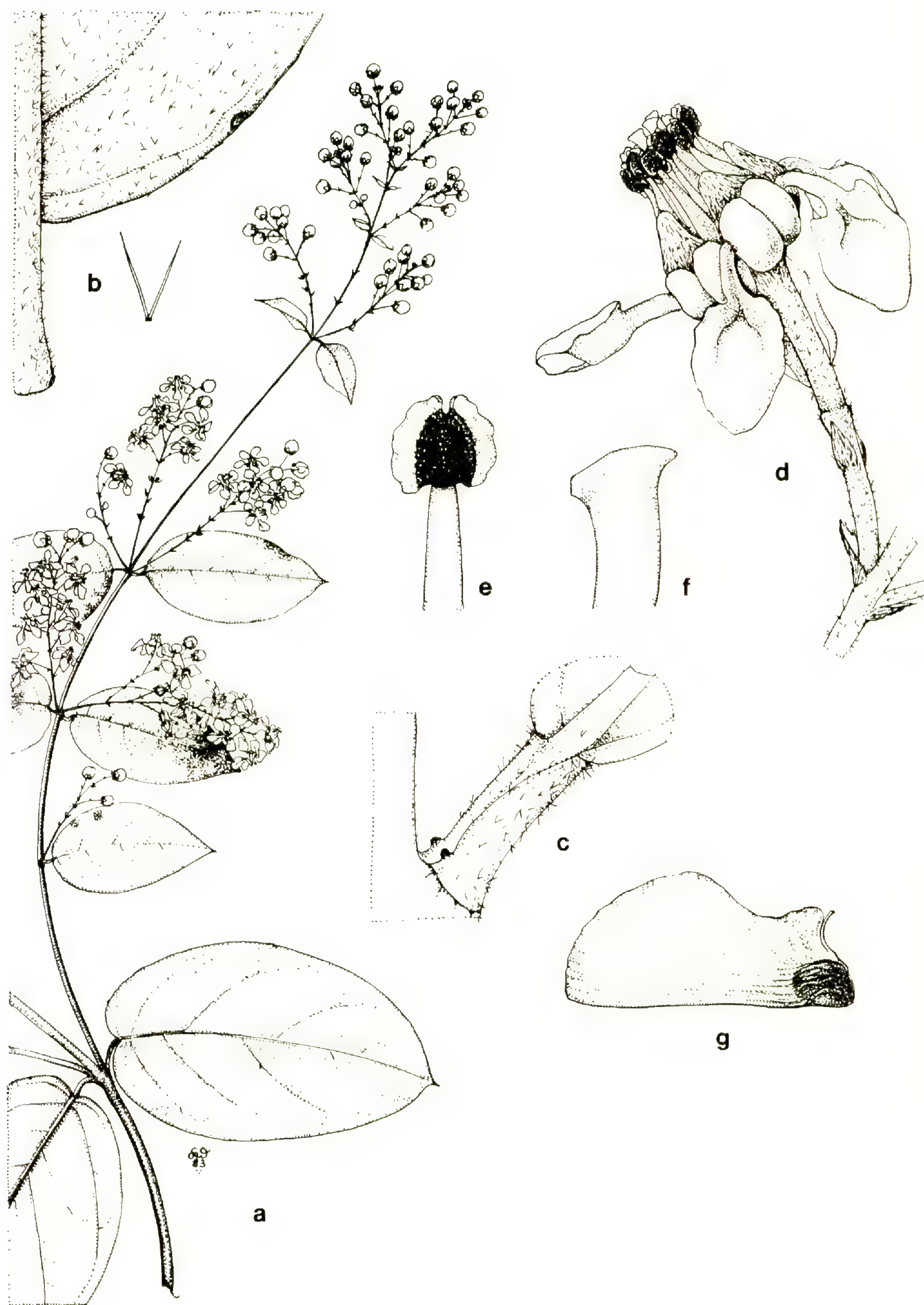


FIG. 8. *Heteropterys aliciae*. a) habit, $\times 0.75$; b) base of leaf, abaxial side, $\times 6$, with hair from abaxial surface, $\times$ ca 40; c) petiole and stipules, $\times 7.5$; d) flower, side view, posterior petal to left, $\times 7.5$; e) anther, abaxial view, $\times 15$; f) apex of style, side view, $\times 30$; g) samara, $\times 1.5$. Drawn by Karin Douthit, a–f from *Anderson et al.* 37119, g from *Anderson et al.* 37118.

margin ca 5 mm above base, the glands sessile or short-cylindrical, ca 0.3 mm in diameter and up to 0.3 mm high; lamina thinly sericeous or subvelutinous to glabrate above, persistently velutinous or subsericeous below, the hairs varying from V-shaped to almost straight and appressed; petiole 3–5 mm long, persistently velutinous or eventually glabrescent; stipules 0.3–0.5 mm long, dark and somewhat glandlike, borne on petiole between base and middle. Inflorescence paniculate, velutinous, the flowers (4–) 6–18 in pseudoracemes 0.8–3 cm long; bracts 1–1.5 mm long, narrowly triangular or elliptical, abaxially sericeous, appressed, eglandular, persistent; peduncle 2.5–3.5 mm long (–7.5 mm in fruit), slightly swollen at apex; bracteoles like bracts but ovate and 0.6–1 mm long, borne between middle and apex of peduncle, sometimes 1 or both apical; pedicel 2.3–3 mm long (–5 mm in fruit). Sepals leaving petals exposed during enlargement of bud, appressed in anthesis, 1.5–2 mm long, 0.9–1.5 mm wide, rounded at apex, abaxially sericeous, adaxially glabrous, the hairs reddish brown; anterior sepal eglandular, lateral 4 all eglandular or all biglandular, the glands ca 1 mm long, green, broadly elliptical or orbicular, flat, not or only slightly compressed. Petals pale yellow, glabrous, the limb abaxially smooth, shallowly concave, entire or slightly erose-denticulate and often somewhat revolute at margin; lateral petals recurved in anthesis, the claw 1.2–1.5 mm long, the limb 2–2.6 mm long, 1.8–2.3 mm wide; posterior petal erect, otherwise hardly different, the claw 1.7–2 mm long, the limb ca 1.7 mm $\times$ 1.7 mm. Filaments glabrous, straight or somewhat recurved distally, 1.6–2.4 mm long, longest opposite anterior sepal, ca $\frac{1}{3}$ – $\frac{1}{2}$ connate; anthers 0.5–0.9 mm long, glabrous or sparsely sericeous, the connective swollen and uniformly dark red to almost black. Ovary sericeous; styles 1.6–2 mm long, glabrous, laterally flattened, the anterior straight, the posterior 2 slightly shorter than anterior, arcuate from base and turned so that all 3 stigmas face posterior petal, truncate or apiculate dorsally at apex. Immature samara 23–33 mm long, thinly sericeous or tomentose; dorsal wing almost as long as samara, 23–30 mm long, 11–15 mm wide, the abaxial margin nearly straight, the adaxial margin flared proximally, then truncate abruptly to nut; nut 7–9 mm long, 5–6 mm high, laterally flattened, without lateral crests or winglets, the longitudinal nerves prominent.

TYPE: BRAZIL. Bahia: Cerrado ca 5 km W of Cocos, near limestone boulders, ca 530 m, 17 Mar 1972 fl, *Anderson et al.* 37119 (UB, holotype; MICH, NY, isotypes).

PARATYPE: BRAZIL. Bahia: Same locality and date as type, fl/fr, *Anderson et al.* 37118 (MICH, NY, UB).

I name this species in honor of Dr. Alicia Lourteig, a good friend and fellow student of the Malpighiaceae. *Heteropterys aliciae* is probably closely related to *H. umbellata* Adr. Juss., which is usually a shrub (but an isotype at P has some clearly twining branches). In *H. umbellata* the leaves are smaller and sericeous to soon glabrate, the leaf glands are peltate and borne on the surface of the lamina, the inflorescence is umbellate or occasionally corymbose, the petals are larger, the styles are rounded dorsally at the apex, and the samaras are smaller.

Heteropterys fluminensis (Grisebach) W. Anderson, comb. nov.

Hiraea fluminensis Grisebach, *Linnaea* 13: 243. 1839.

Mascagnia fluminensis (Grisebach) Grisebach in Martius, *Fl. Bras.* 12(1): 94. 1858.

Slender woody vine, the stems sericeous to soon glabrate. Lamina of larger leaves 3.8–8 cm long, 1.2–3.5 cm wide, elliptical, cuneate to rounded at base, mostly acute or very abruptly short-acuminate at apex, initially sericeous but soon nearly to quite glabrate, bearing below a row of small impressed glands parallel to but set in from the margin; petiole 4–13 mm long, sericeous to glabrate, eglandular or biglandular at base, often both on the same plant; stipules minute, triangular, borne on stem beside petiole, or absent. Flowers borne in 4-flowered umbels; bracts 1–1.5 mm long, eglandular; peduncle 4–11 mm long; bracteoles apical, 1–1.5 mm long, dissimilar, 1 straight and eglandular, the other falcate and bearing a large eccentric abaxial gland (or occasionally both bracteoles 1-glandular); pedicel 2.5–4 (–6) mm long, shorter than peduncle in flower, elongating somewhat in fruit, usually slightly curved, thicker than peduncle and notably swollen distally, sericeous to glabrescent. Flowers small, ca 10–14 mm in diameter. Sepals abaxially densely sericeous, adaxially glabrous, somewhat revolute at apex and often at sides in anthesis, the anterior eglandular, the lateral 4 biglandular. Petals yellow, glabrous, the lateral 4 entire or erose, the posterior bearing small marginal glands on proximal $\frac{1}{2}$ or all around limb. Stamens 10, alike; filaments glabrous, partly connate; anthers reflexed in anthesis, the locules densely pilose. Styles 3, erect, straight, with internal stigmas and dorsally truncate at apex, the anterior slightly shorter and slenderer than the posterior 2. Samara 20–25 mm long, the wing 7–10 mm wide; nut cylindrical, ca 7–8 mm $\times$ 2 mm, without lateral crests but with many very prominent parallel longitudinal nerves.

TYPE: BRAZIL. Rio de Janeiro: Near the city of Rio de Janeiro, *Sellow*. According to Niedenzu (1928, p. 118), Sellow collected the species twice, in 1814 and 1818. Both specimens were probably at B, and Grisebach would have studied both, so they should be considered syntypes. The 1814 syntype is shown in F negative 12688. I do not know whether either syntype is represented now by a duplicate at GOET or elsewhere.

SPECIMENS STUDIED. BRAZIL. Rio de Janeiro: Restinga de Grumará, Aug fl/fr, *Araújo 106* (NY); Serra do Orgão, primary forest, Sep fl, *Occhioni 6064* (MICH); Jacarépaguá, Oct fl/fr, *Pereira 4354* (F); Mpio Cabo Frio, restinga opposite Manguinhos beach, Sep fl, *Souza 128/Scott 5* (MICH). Espírito Santo: Mpio Jaguaré, Agua Limpa, edge of forest, Oct fl, *Hatschbach 46977* (MICH).

Grisebach and Niedenzu both realized that this species was anomalous in *Mascagnia*, and the fruiting collections now available show that it is a *Heteropterys*. I cannot match it to any species in Niedenzu's 1928 treatment of *Heteropterys*. It seems to be closest to *H. leschenaultiana* Adr. Juss., an affinity that Grisebach noted in 1858. The two both have the petioles often biglandular at the base, flowers in umbels of four, and revolute sepals. However, in *H. leschenaultiana* the leaves are larger, the laminar glands are marginal or nearly so, the bracteoles are eglandular, the pedicel is longer than the peduncle and not or hardly inflated, the anthers are glabrous, and the nut of the samara is more typical for the genus, i.e., plumper, shorter, and with less prominent nerves.

***Heteropterys huberi* W. Anderson, sp. nov.**

Frutex erectus usque ad 4 m altus. Foliorum majorum lamina 5–8 cm longa, 2.5–4.5 cm lata, apice obtusa vel rotundata et interdum emarginata, coriacea, subtus serie inframarginali 6–12 glandularum instructa et dense et pertinaciter sericea pilis primo rufis demum canescentibus, reticulo utrinque prominulo et

visibili; petiolus 1–4 mm longus, eglandulosus vel biglandulosus. Inflorescentiae elongatae, saepe folia subtendentia superantes, floribus in umbellis 4-floris saepe pari proximali subtentis. Sepala revoluta, utrinque appresso-tomentosa. Petala lutea. Antherarum connectivum basi atrorubrum distaliter luteum. Samara immatura 12–14 mm longa.

Shrub up to 4 m tall; stems sericeous, eventually glabrate. Leaves mostly decussate; lamina of larger leaves 5–8 cm long, 2.5–4.5 cm wide, elliptical, obtuse or rounded at base, obtuse or rounded and sometimes emarginate at apex, coriaceous, bearing an inframarginal row of 6–12 glands below on each side, thinly whitish-sericeous to eventually glabrate above, densely and $\pm$ persistently sericeous below with the hairs very short, straight, sessile, strongly appressed, initially reddish brown but fading with age, the reticulum about equally prominent and readily visible on both sides; petiole 1–4 mm long, sericeous, eglandular or biglandular near middle; stipules not seen. Inflorescences axillary and terminal, paniculate, long-stalked and open, often longer than subtending leaves, sericeous, the flowers in terminal umbels of 4, often with an additional pair borne below and separated from the umbel; bracts and bracteoles 1–1.5 mm long, narrowly elliptical, appressed or involute, eglandular or the bracteoles with 2 marginal glands; peduncle 1–2 mm long; pedicel 4–7.5 mm long. Sepals completely concealing petals during enlargement of bud, revolute in anthesis, 3 mm long, 1.2–1.5 mm wide, triangular, appressed-tomentose on both sides but more densely and uniformly so abaxially, the hairs dark brown; anterior sepal eglandular, lateral 4 biglandular, the glands 1.3 mm long, elliptical. Petals yellow, glabrous or sparsely pilose on margin, abaxially smooth; lateral petals with the claw 2 mm long, the limb circular, ca 3 mm in diameter, erose; posterior petal hardly different, the claw ca 2.5 mm long, the limb slightly narrower and glandular-dentate near base. Filaments glabrous, straight or slightly curved, 2.1–2.5 mm long opposite sepals, 1.5–2 mm long opposite petals, basally connate; anthers 0.5–0.8 mm long, glabrous, the connective with a dark red spot just above insertion of filament, otherwise yellow. Ovary 1 mm high, sericeous; styles 1.8–2 mm long, glabrous, straight, divergent from base, truncate at apex. Immature samara 12–14 mm long, persistently reddish brown-sericeous; dorsal wing as long as samara, 5–5.5 mm wide, the abaxial margin curved upward; nut 3–3.5 mm long, 2–2.5 mm high, without lateral crests or winglets.

TYPE: VENEZUELA. Terr. Fed. Amazonas: Depto. Río Negro, arbustales, roca abierta y bosque bajo denso en la vertiente oriental del Macizo Aracamuni, 01°32'N, 65°48'W, 750 m, 10 Feb 1981 imm fr, *Huber & Medina 5893* (MICH, holotype).

PARATYPE: VENEZUELA. Terr. Fed. Amazonas: Depto. Río Negro, pequeña altiplanicie de arenisca, lado derecho (oriental) del Río Siapa o Matapire, poco arriba de su salida del Macizo Aracamuni, 01°36'N, 65°41'W, 600 m, Feb fl, *Huber 6010* (MICH).

Heteropterys huberi is referable to subgenus *Parabanisteria*. In my Guayana Highland treatment (Anderson 1981) it will key to *H. cuatrecasasii* W. Anderson, which it does resemble in its umbellate inflorescences and densely sericeous leaves, but the two species are easily distinguished. *Heteropterys cuatrecasasii* is a plant from higher elevations on the Cerros Parú, Huachamacari, and Marahuaca, which lie about 2–3° to the north of Cerro Aracamuni. It is a woody vine; its leaves are acuminate at the apex, bear few or no glands, and have the reticulum

nearly or quite invisible above; the petiole of larger leaves is 5–9 mm long; the inflorescences are short-stalked and crowded, mostly shorter than the subtending leaves; and the connective of the anthers is uniformly dark. I suspect that the species most closely related to *H. huberi* is *H. atabapensis* W. Anderson, a shrub of lower elevations, which differs from *H. huberi* in having its leaves very soon glabrate and inflorescences racemose.

This species is named in honor of Dr. Otto Huber, collector of the two known collections, in recognition of his contributions to our knowledge of the flora of southern Venezuela.

***Heteropterys prunifolia* (H. B. K.) W. Anderson, comb. nov.**

Hiraea? prunifolia H. B. K., Nov. Gen. Sp. 5 (quarto ed.): 170. 1821 [1822].

Study of the type (herb. Humb., P!) shows that this is an older name for *Heteropterys rhombifolia* Rusby.

***Heteropterys standleyana* W. Anderson, nom. nov.**

Banisteria rosea Standley, J. Wash. Acad. Sci. 14: 96. 1924, non *Heteropterys rosea* Kralik, Akad. Wiss. Wien, Math.-Naturwiss. Kl., Denkschr. 79: 281. 1908.

This is one of the pink-flowered species of *Heteropterys*, which form a difficult complex in Mexico and Central America. It differs from other Central American pink-flowered species in the following combination of characters: Vegetative leaves soon glabrate; inflorescences usually produced on stems lacking vegetative leaves, loosely tomentose or appressed-tomentose, gradually glabrescent in a patchy manner; nut of samara smooth-sided, quite without crests or winglets. See my forthcoming treatment in the Flora de Nicaragua for a longer description.

SPECIMENS STUDIED. GUATEMALA. El Progreso: Sierra de Las Minas, dry barranca of Río Frio, between Tulumajillo and Finca Montañita in foothills, 330–500 m, Feb fl/fr, *Steyermark* 43351 (F, NY).—EL SALVADOR. La Unión: Vicinity of La Unión, dry thicket, 150 m or less, Feb fl, *Standley* 20653 (NY). San Vicente, vicinity of San Vicente: In quebrada, 350–500 m, Mar fr, *Standley* 21663 (NY, isotype; US, holotype); dry brushy hillside, 400–500 m, Feb fl, *Standley & Padilla* 3476 (F). Santa Ana: Vicinity of Metapán, 370 m, dry brushy rocky hillside, Jan/Feb fl/fr, *Standley & Padilla* 3055 & 3208 (both F).—HONDURAS. Choluteca: Rocky area, near Río Pespire, 38 m, Feb fl, *Williams & Molina* 15570 (F). Morazán: Between San Buenaventura and El Sauce, area of pines, 1300 m, Feb fl, *Williams & Molina* 15575 (F).—NICARAGUA. Matagalpa: E of Puertas Viejas, 400–500 m, Feb fl/fr, *Moreno* 20100 (MICH) & 20111 (MO). Managua: 20 km NE of Tipitapa, 60 m, Sep ster, *Danin* 76-16-13 (MICH). Masaya, Parque Nacional Volcán Masaya: NW sector of caldera, dry forest on lava flow, 300 m, Jan fl, *Neill* 3135E (MICH, MO); NE side of El Comalito, deciduous forest on lava, 325 m, Feb fl/fr, *Stevens* 6269 (MICH).

***Janusia christianeae* W. Anderson, sp. nov.**

Fig. 9.

Planta volubilis, caulibus primo aureosericeis mox albotomentosis demum glabratibus. Foliorum majorum lamina 4.5–6 cm longa, 2.2–3 cm lata, ovata vel paene elliptica, basi rotundata vel subcordata, apice obtusa, acuta, vel parum acuminata et saepe mucronata, supra tomentosa mox glabrata reticulo prominenti, subtus dense et pertinaciter subsericea vel appresso-tomentosa; petiolus 3–10 mm longus. Flores omnes chasmogami, in umbellis axillaribus 4-floris portati, bracteis 3.5–5.5 mm longis et deciduis, pedunculo 8–15 mm longo, bracteolis 3–5 mm longis, subulatis vel linearibus, prope medium pedunculi portatis, plerumque ante vel per anthesin deciduis, pedicello 9–13 mm longo. Sepala abaxialiter dense sericea pilis rufo-aureis praeter zonam marginalem albotomentosam. Petala gla-



FIG. 9. *Janusia christianeae*. a) flowering branch and large leaves, $\times 0.5$; b) base of leaf and node, $\times 5$; c) flower, oblique-anterior view, $\times 1$; d) right-handed flower, anterior view, with 2 sepals and 4 lateral petals removed, $\times 2.5$, and deciduous bracteole to left, $\times 5$; e) anther, abaxial side, $\times 5$; f) immature fruit with only 2 samaras enlarging, sepals removed, $\times 1.5$. Drawn by Karin Douthit, a-e from Anderson *et al.* 36829, f from Hatschbach 42315.

bra, laciniata, 4 lateralia ungue 2–3 mm longo, limbo 12–14 mm longo latoque et eglanduloso, posticum ungue 5 mm longo, limbo 10 mm longo, 11 mm lato, basi glandulifero. Stamina 6, valde heteromorpha, anticum et 1 antico-laterale maxima et valde arcuata, alterum antico-laterale et 3 postica minima; antherae sericeae vel pilosae, connectivo eglanduloso. Stylus 1, excentricus, cum stamine magno antico-laterali arcuatus. Samara immatura basi brevirostrata.

Vine twining in shrubs; stems initially densely sericeous with an overstory of golden hairs and an understory of white hairs, soon becoming tomentose as outer hairs fall and inner hairs spread, eventually glabrate and dark red or purplish, finally brown and lenticellate. Lamina of larger leaves 4.5–6 cm long, 2.2–3 cm wide, ovate to almost elliptical, rounded or slightly cordate at base, obtuse, acute, or slightly acuminate and often mucronate at apex, initially tomentose above but soon glabrate with some hairs often persistent proximally on midrib, densely and persistently subsericeous or appressed-tomentose below with the long, fine, stramineous hairs subsessile or short-stalked, straight or sinuous, appressed or somewhat spreading, the lateral veins and reticulum prominent above; petiole 3–10 mm long, densely and persistently sericeous or tomentose, bearing at or just above or below apex 2 sessile or subsessile disciform glands 0.5–0.8 mm in diameter, these sometimes on base of lamina just above apex of petiole; stipules 0.5–1 mm long, narrowly triangular or subulate, borne on stem at base of petiole. Flowers all chasmogamous, borne in 4-flowered umbels, the umbels mostly axil-

lary and single, subsessile or raised on a common stalk up to 13 mm long and usually bearing 2 bracts or small leaves; floriferous bracts [subtending floriferous peduncles] 3.5–5.5 mm long, narrowly triangular, loosely sericeous, deciduous before or during anthesis; peduncle 8–15 mm long (–23 mm in fruit), 0.4–0.6 mm in diameter, white-tomentose; bracteoles 3–5 mm long, subulate or linear, loosely sericeous, borne near middle of peduncle, mostly at different heights, somewhat spreading, mostly deciduous before or during anthesis; pedicel 9–13 mm long, proximally slender like peduncle but distally enlarged and often 2–3 mm in diameter at apex, proximally white-tomentose or -sericeous, distally golden-sericeous. Flowers ca 35 mm in diameter. Sepals 5–5.3 mm long, 3–3.3 mm wide, quite distinct, ovate, obtuse at apex, strongly incurved or inrolled in anthesis, abaxially densely and persistently sericeous with the hairs reddish golden except for a marginal band of white hairs, adaxially finely white-sericeous in proximal half and glabrous in distal half, the anterior eglandular or bearing 1 or 2 glands smaller than those of lateral sepals, the lateral 4 biglandular, the glands 3–3.5 mm long, 1.1–1.5 mm wide, narrowly elliptical, attached their whole length, separated (i.e., not compressed). Petals orange-yellow, glabrous, deeply laciniate or fimbriate-laciniate, eglandular except for gland-tipped divisions on base of limb and claw of posterior petal; 4 lateral petals widely spreading, the claw 2–3 mm long, the limb flat or slightly concave, roughly circular except for the broadly cuneate base, 12–14 mm long and wide; posterior petal with the thick, winged claw erect, 5 mm long, the limb reflexed, subcircular, 10 mm long, 11 mm wide. Stamens 6, 5 opposite sepals and designated like sepals as anterior (1), anterior-lateral (2), and posterior-lateral (2), plus 1 posterior, opposite posterior petal, all with glabrous and quite distinct filaments and all fertile (or at least antheriferous), but dramatically heteromorphic, with 2 very large and the other 4 very small; anterior stamen and 1 of the anterior-lateral stamens large, the filaments very thick (1 mm in diameter at base), ca 8 mm long, strongly bowed, that of the anterior-lateral stamen bent diagonally across flower to ascend between lateral sepals and in front of a posterior-lateral petal; filament of anterior stamen bent in front of the other large stamen, across flower to arise in front of the other posterior-lateral petal; anthers of large stamens 1.7–1.8 mm long, reflexed and bent sideways so that pollen is presented toward center of flower, the locules densely sericeous and containing much pollen, the ovate connective not exceeding locules and without an apical gland; 4 small stamens displayed in center of flower between tips of sepals, with slender filaments 0.5 mm in diameter at base and 0.2–0.3 mm at apex and anthers 0.7–1 mm long, $\pm$ reflexed, the short locules containing some pollen (but indehiscent?) and somewhat pilose, the connective mostly exceeding locules and acute but without an apical gland; small anterior-lateral stamen with filament 3.5 mm long and bent in same direction as large adjacent anterior stamen; other small stamens in a posterior group, all leaning forward toward anterior sepal, the posterior-lateral 2 with filaments ca 2.5 mm long, the posterior 1 with filament ca 1.5 mm long. Carpels 3, 1 anterior and 2 posterior, hairy; style 1, borne on anterior carpel, glabrous, stout (ca 0.8 mm in diameter at base), ca 10 mm long, strongly bowed, bent to 1 side, curving with (outside of) filament of large anterior-lateral stamen, tapering to a pointed apex with the small, flat, elliptical stigma displaced to 1 side so that it points upward, away from the adjacent anther. See notes below for discussion of floral symmetry. Samaras separating from a low, rounded or obscurely 3-sided torus ca 1 mm high; very immature samara loosely sericeous with the proximal hairs white and the distal ones golden;

nut without crests radiating from areole; lateral winglets restricted to base of nut, connate, forming a flattened decurved apparent extension of nut ("rostrum") 2 mm long and 1 mm wide; cartilaginous carpophore extending from receptacle down line of fusion of lateral winglets; full-sized samaras not seen.

TYPE: BRAZIL. Bahia: Mpio Cristopolis, Eng° Velho, cerrado, 800 m, 17 Jul 1979 fl/imm fr, *Hatschbach* 42315 (MBM, holotype; MICH, isotype).

PARATYPES: BRAZIL. Bahia: Espigão Mestre, ca 100 km WSW of Barreiras, brushy cerrado, 750–800 m, Mar fl, *Anderson et al.* 36829 (UB); BR-020, 100 km W of Barreiras, caatinga, Oct fl, *Hatschbach* 45010 (MICH).

I am pleased to dedicate this handsome and distinctive species to a fine taxonomist, Christiane Eva Seidenschnur Anderson. *Janusia christianeae* is related to several other species that have more or less heteromorphic stamens and a style that curves right or left. Of those, *Janusia anisandra*, *J. caudata*, and *J. malmeana* have androecia similar to that of *J. christianeae* but are immediately set off by their advanced inflorescences, in which the ancestral four-flowered umbel has been reduced mostly to a single flower subtended by several bracts; *J. anisandra* differs further in having tomentose leaves, and the other two in having sessile pedicels. In *J. hexandra* and *J. occhionii* the flowers are pedunculate and borne in umbels as in *J. christianeae*, but the androecium has the posterior-lateral stamens larger than both the anterior-lateral ones; moreover, the bracts are short and persistent, the bracteoles are short, apical, and persistent, and the anthers bear an apical gland.

As Figure 9 shows, the flower in this species gives an impression of bilateral symmetry that is probably acceptable to a bee, but a botanist sees it as irregular, not symmetrical about a plane of symmetry passing through the anterior sepal and posterior petal, as is usual in the family. Not only are the style and anterior stamen strongly displaced sideways, but the two anterior-lateral stamens are very dissimilar. The flower shown in Figure 9 is right-handed, i.e., the style bends to the right as one faces the posterior petal. The same plants also make left-handed flowers, in which 1) the style bends to the left; 2) the large anterior stamen bends to the right; 3) the other large stamen is the anterior-lateral one to the right of the anterior stamen, and bends to the left; and 4) the anterior-lateral stamen to the left of the large anterior stamen is small and bends to the right with the anterior one. Right- and left-handed flowers are mirror-images of each other, and in the few cases studied two flowers in each umbel of four were right-handed and two left-handed, with opposite members of each pair mirror-images. However, I need to examine much more material before I can say with confidence that the distribution is consistent.

***Janusia hexandra* (Vell.) W. Anderson, comb. nov.**

Banisteria hexandra Vell., Fl. Flum. 188 [text]. 1825 [1829]; vol. 4 pl. 149 [icones]. 1831.

In both the text and the plate Vellozo described this plant as having six stamens and one female part [i.e., one style]. Since his plant was clearly not a *Camarea*, it must have been a *Janusia* (*Schwannia* in the sense of Jussieu and Niedenzu). The habitat given was maritime forests, presumably in the area of Rio de Janeiro. The only species of *Janusia* found in that habitat, or indeed anywhere in the area of Rio, is *J. muricata* (Adr. Juss.) Grisebach [*Schwannia muricata*

(Adr. Juss.) Adr. Juss., based on *Fimbriaria muricata* Adr. Juss., 1840]. The characters that can be gleaned from Vellozo's brief description and crude drawing fit *J. muricata* well. The leaf shape is acceptable, the flowers are in umbels, and the petals are "dentate," a reasonable approximation to the actual condition, which is fimbriate. Especially significant are the petiole glands, which are knobby and often borne below the apex, as in *J. muricata*. Finally, I am intrigued by Vellozo's statement that the petiole is biglandular "hinc, et illinc." "Hinc . . . illinc" usually means "on one side . . . on the other," but in this case the author may have meant at both ends, referring to the glandular enlargement of the stipules that is common in *J. muricata*. The identity of Vellozo's plant seems clear, and I see no alternative to adopting his name in place of the later epithet *muricata*.

Janusia occhionii W. Anderson, sp. nov.

Fig. 10.

Planta volubilis lignosa, caulibus laxe sericeis vel appresso-tomentosis demum glabratis. Foliorum majorum lamina 4.5–7 (–10) cm longa, 2.6–4.2 (–5.3) cm lata, plerumque ovata, basi rotundata vel subcordata, apice rotundata vel obtusa et plerumque mucronata vel brevicuspidata, supra mox glabrata, subtus dense et pertinaciter laxe sericea vel tomentosa et basi juxta costam biglandulosa; petiolus 6–11 mm longus; stipulae 1–1.5 mm longae, triangulares. Flores omnes chasmogami, in umbellis axillaribus 4-floris portati, bracteis 1.3–2.5 mm longis persistentibusque, bracteolis 1–2 mm longis, apicalibus, persistentibus. Petala glabra vel in ungue sericea, dentata, laciniata, vel brevifimbriata, 4 lateralialia ungue 2–3 mm longo, limbo 7.5–9 mm longo, 7.5–10 mm lato, posticum ungue alato 6 mm longo et glanduloso-fimbriato, limbo 6 mm longo, 7–8.5 mm lato. Stamina 6, heteromorpha, anticum et 2 postico-lateralialia filamentis longioribus arcuatisque, posticum et 2 antico-lateralialia filamentis brevioribus subrectisque; antherae pilosae, connectivo glanduloso. Stylus 1, excentricus, valde arcuatus. Samara basi rostrata rostro 2–3.5 mm longo, 1.5–3 mm lato.

Woody vine twining in shrubs, or forming a shrub when nothing is available to climb on; stems densely but loosely sericeous or appressed-tomentose with somewhat spreading hairs, eventually glabrate, purplish, lenticellate. Lamina of larger leaves 4.5–7 (–10) cm long, 2.6–4.2 (–5.3) cm wide, ovate or occasionally elliptical, rounded or subcordate at base, rounded or obtuse and mostly mucronate or short-cuspidate at apex, initially loosely sericeous above but soon glabrate with some hairs usually persistent proximally on midrib, densely and persistently loosely sericeous to tomentose below with the long, fine, stramineous or white hairs subsessile or short-stalked, straight or sinuous to strongly twisted and appressed to strongly spreading, bearing below at base beside midrib 2 sessile or subsessile disciform or cupshaped glands 0.6–1.2 mm in diameter, the reticulum prominulous above, the lateral veins prominent below; petiole 6–11 mm long, densely and persistently subsericeous or tomentose, eglandular; stipules 1–1.5 mm long, triangular, borne on stem between petioles, thick, persistent. Flowers all chasmogamous, borne in 4-flowered umbels, the umbels axillary to full-sized or smaller leaves, raised on a stalk (5–) 10–25 mm long and bearing at its apex 2 much-reduced leaves ("bracts") bearing 2 abaxial glands, these bracts often deciduous, the umbels single or occasionally 2 (1 above the other) in the same axil; inflorescence with vestiture like that of stems; floriferous bracts [subtending floriferous peduncles] 1.3–2.5 mm long, ovate, abaxially sericeous, adaxially glabrous, persistent; peduncle 3–10 mm long (–15 mm in fruit), often of 2 lengths in the

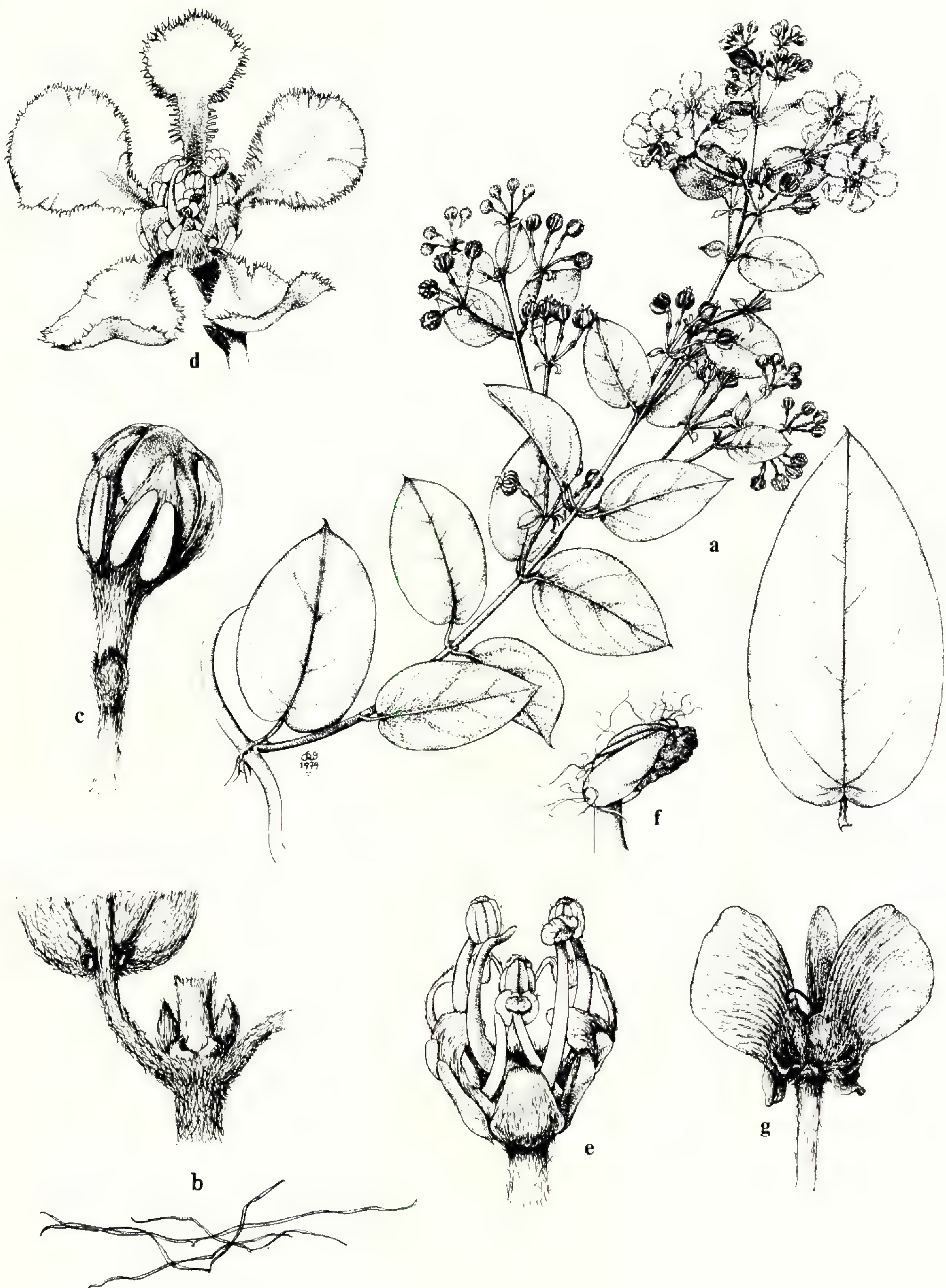


FIG. 10. *Janusia occhionii*. a) flowering branch and large leaf, $\times 0.5$; b) base of leaf and node, $\times 2.5$, with enlarged hairs from abaxial surface of lamina, $\times 25$; c) flower bud, $\times 3.5$; d) left-handed flower, oblique-anterior view, $\times 2$; e) flower, anterior view, petals removed, $\times 4$; f) anther, side view, $\times 15$; g) fruit, anterior samara in middle, sepals removed, $\times 1.5$. Drawn by Karin Douthit from Anderson 11151 except large leaf, from Hatschbach 21590.

same umbel; bracteoles like bracts but 1–2 mm long, apical, persistent; pedicel 3–7 mm long, slightly thickened distally. Flowers 22–25 mm in diameter. Sepals 4.5–5 mm long, 2–2.5 mm wide, quite distinct, narrowly ovate, obtuse or acute at apex, strongly incurved or inrolled in anthesis, abaxially densely and persistently sericeous with the hairs stramineous except white just on the membranous margin, adaxially densely white-sericeous in proximal $\frac{1}{2}$ – $\frac{2}{3}$ and glabrous distally, the anterior eglandular, the lateral 4 biglandular, the glands 3–4 mm long, 0.7–1 mm wide, narrowly elliptical, attached their whole length, separated (i.e., not compressed). Petals orange-yellow, glabrous except loosely white-sericeous on claw of posterior petal and rarely on claws of lateral petals, dentate or lacinate to short-fimbriate, eglandular except for gland-tipped processes on winged claw of posterior petal, widely spreading and $\pm$ flat or the anterior 2 with limbs cupped upward; 4 lateral petals with the claw 2–3 mm long, the limb oblate or obovate or roughly circular except for the broadly cuneate base, 7.5–9 mm long, 7.5–10 mm wide; posterior petal with the thick, distally winged claw 6 mm long, the limb oblate, 6 mm long, 7–8.5 mm wide. Stamens 6, 5 opposite sepals and designated like sepals as anterior (1), anterior-lateral (2), and posterior-lateral (2), plus 1 posterior, opposite posterior petal, all with glabrous and quite distinct filaments and all fertile but heteromorphic, generally 3 long and 3 short; anterior stamen long, the filament thick (ca 0.7 mm in diameter at base), 5.5–6 mm long, bent to left or right to raise anther in front of 1 of the adjacent anterior-lateral petals, distally bowed; 2 anterior-lateral stamens short, with slender filaments (ca 0.4 mm in diameter at base), 3–4 mm long, alike or the 1 from which the anterior bends away longer, straight or slightly bowed, both leaning sideways toward center of flower to present anthers $\pm$ on midline between anterior sepal and posterior petal; 2 posterior-lateral stamens long, the filament thick like the anterior and about as long or slightly shorter, (4.5–) 5–5.5 mm long, alike or the 1 on same side as the anterior longer, leaning sideways to raise anther in front of the adjacent posterior-lateral petal, distally bowed; posterior stamen short, similar to the anterior-lateral 2, the filament 2.5–3 mm long, straight, leaning forward on midline toward anterior sepal; anthers alike or subequal, borne reflexed on long filaments and erect or reflexed on short filaments, 1–1.4 mm long, moderately to densely spreading-pilose on locules, the connective distally enlarged into a spherical or hemispherical dark red gland usually extending beyond locules. Carpels 3, 1 anterior and 2 posterior, hairy; style 1, borne on anterior carpel, glabrous, stout, ca 6 mm long, leaning to right or left (away from anterior stamen) to stand in front of the other anterior-lateral petal, strongly bowed and bent ca 90° near apex, the small apical stigma held in center of flower between anthers of the 3 long stamens. See notes below for discussion of floral symmetry. Samaras separating from a short pyramidal torus ca 2 mm high; samara 15–20 mm long, sericeous on nut and proximally on wing; dorsal wing 11–14 mm long, 6–8 mm wide, with a rounded or triangular projection 0.5–2 mm high at adaxial base; nut ca 2–3 mm high, 2.5–4 mm long, bearing several parallel ribs, low crests, or dissected outgrowths 0.2–0.8 mm high radiating from areole; lateral winglets restricted to base of nut, connate, forming a straight or decurved apparent extension of nut (“rostrum”) 2–3.5 mm long and 1.5–3 mm wide; cartilaginous carpophore well developed and functional, extending from receptacle down line of fusion of lateral winglets. Chromosome number: $n = 20$ (counted in *Anderson 11151* and *11175*).

TYPE: BRAZIL. Mato Grosso do Sul: 65 km by road S of Naviraí, shrubby secondary growth at edge of forest, 23 Mar 1974 fl/fr, *Anderson 11175* (UB, holotype; MICH, NY, isotypes).

PARATYPES: BRAZIL. Paraná: Fazenda Lagôa, ca 20 km N of Cianorte, dense cerrado on sandy soil, Mar fl/fr, *Anderson 11151* (MICH, NY); Mpio Campo Mourão, airport road, cerrado, 625 m, Feb fl/fr, *Hatschbach 8852* (MBM, MICH, NY, P, US); Mpio Cianorte, Fazenda Lagôa, cerrado, Apr fl/fr, *Hatschbach 14253* (F, MBM, MICH, NY, P, US), May fl/fr, *Hatschbach 21590* (MBM, MICH, P); Sabauldia, cerrado, *R. Hertel s.n.* in 1946 (P); Fazenda Lagôa, S of Rio Ivaí, ca 15 km E of São Tomé, cerrado, reddish sand, 240 m, Apr fl/fr, *Lindeman & Haas 979* (MBM, NY, US). Mato Grosso do Sul: Mpio Iguatemi, Rio Piraí, woodland with sandy soil, Dec fl, *Hatschbach 45853* (MICH); vicinity of Sapucaia, edge of low forest with sandy soil, Feb fl, *Hatschbach 46204* (MICH).—PARAGUAY. Amambay: Parque Nacional Cerro Cora, roadside secondary growth, 175 m, Mar fl, *Simonis et al. 114* (MICH).

The epithet of *Janusia occhionii* honors Dr. Paulo Occhioni, Professor of Botany at the Universidade Federal do Rio de Janeiro. For many years Professor Occhioni has advanced systematic botany in Brazil through teaching, collecting, encouraging students, and publishing the journal LEANDRA. He has been a gracious host to many visiting botanists, including me, and I am happy to express my gratitude to a fine gentleman and good friend.

Janusia occhionii is a member of the group of species discussed above under *J. christianeae*, which see. It is most closely related to *J. hexandra*, a species of the vicinity of Rio de Janeiro and coastal areas north of there into Bahia. *Janusia hexandra* differs from *J. occhionii* most obviously in its leaves, which are usually cuneate at the base and always very tightly sericeous below with the fine hairs sessile, straight, strongly appressed, and parallel. This tendency toward finer appressed vesture is also evident on the petioles, stems, and inflorescence axes. The petals of *J. hexandra* are smaller and more deeply fimbriate than in *J. occhionii*, its short-stalked leaf glands are often on the petiole instead of the base of the lamina, and its stipules often enlarge into flattened glandular masses in age.

The flowers of *Janusia occhionii* are less irregular than those of *J. christianeae*. In this species the four lateral stamens usually maintain bilateral symmetry as two mirror-image pairs, a short anterior pair and a longer posterior pair. Occasional flowers have the members of those pairs unequal, but the general pattern remains nearly symmetrical. The posterior stamen is unpaired but lies on the plane of symmetry. The irregularity stems from the fact that the unpaired anterior stamen bends to the left or right, out of the plane of symmetry, and the style bends the other way. Right- and left-handed flowers occur in the same umbels.

***Janusia prancei* W. Anderson, sp. nov.**

Fig. 11.

Planta volubilis ramis sericeis demum lignosis. Foliorum majorum lamina 6–11 (–13) cm longa, 3–5.5 cm lata, plerumque elliptica, basi truncata, rotundata, vel subcordata, apice obtusa, rotundata, vel emarginata et plerumque mucronata, supra glabrescens, subtus pertinaciter sericea et basi juxta costam biglandulosa; petiolus (5–) 7–12 mm longus, eglandulosus. Flores omnes chasmogami, zygomorphi, in umbellis axillaribus 4-floris portati; umbella 2 bracteis biglandulosis subtenta; pedunculus florifer nullus; pedicellus 4–7 mm longus. Petala aurantiaca, glabra, unguibus integris, limbis fimbriato-laciniatis. Stamina 6; filamenta sepalis opposita 5–7 mm longa, petalo postico oppositum 3–4 mm longum; antherae 1–1.5 mm longae, tomentosae. Stylus 1, 6–7.5 mm longus, arcuatus et apice abrupte flexus, stigmatate laterali ellipticoque. Samarae erectae parallelaeque; nux lateribus laevis basi rotundata erostrata.

Twining vine with the older stems becoming woody, or a shrub when nothing is available to climb on; stems densely and tightly sericeous, only the woody older

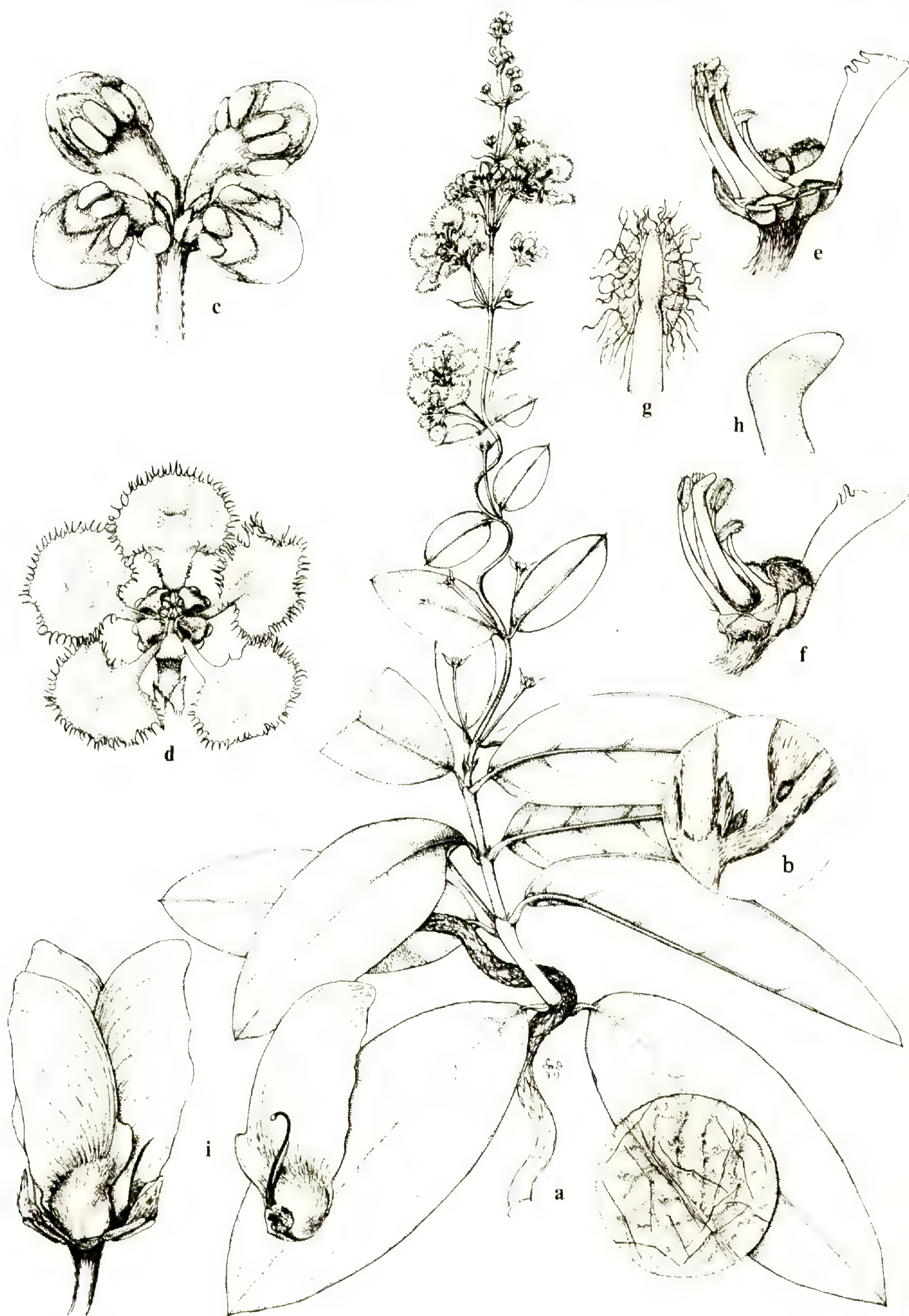


FIG. 11. *Janusia prancei*. a) habit, $\times 0.5$, with adaxial surface of lamina enlarged, $\times 6$; b) base of leaf and node, $\times 1.5$; c) umbel in bud, $\times 2.5$; d) flower, oblique-anterior view, $\times 1.5$; e) flower, side view, cut away to show androecium, with claw of posterior petal to right, $\times 2.5$; f) same as e, but with 2 lateral stamens removed to show style, $\times 2.5$; g) anther, abaxial side, $\times 10$; h) stigma, $\times 10$; i) immature fruit, anterior view, and separate anterior samara, $\times 2.5$. Drawn by Karin Douthit, a–c and i from *Prance 13770*, d–h from *Anderson 12334*.

stems glabrescent. Lamina of larger leaves 6–11 (–13) cm long, 3–5.5 cm wide, elliptical or slightly ovate, truncate, rounded, or subcordate at base, obtuse, rounded, or emarginate and usually mucronate at apex, initially sericeous above but soon glabrescent with some hairs usually persistent at least proximally, densely and persistently sericeous below with the long fine hairs generally straight and appressed but with some sinuous and/or spreading to give a somewhat loose overall effect, this becoming more marked in older leaves, bearing below at or just above base against midrib 2 flat sessile elliptical glands ca 2 mm long and 0.7–1 mm wide, the lateral veins and reticulum prominent above, the lateral veins prominent below; petiole (5–) 7–12 mm long, densely and persistently sericeous, eglandular; stipules 0.5–1 mm long, triangular, borne on stem beside petioles. Flowers all chasmogamous, borne in 4-flowered umbels, the umbels axillary to reduced leaves that are smaller at successive nodes and may be only “bracts” distally, mostly 2–3 per axil in a vertical rank with the oldest adaxial, raised on a stalk (3–) 7–25 mm long and bearing at its apex 2 persistent much-reduced leaves (“bracts”) bearing 2 large abaxial glands; inflorescence with vestiture like that of stems; floriferous bracts and bracteoles 1–2.5 mm long, triangular or ovate, abaxially sericeous, adaxially glabrous, stiff and erect, persistent; peduncle absent, the bract and 2 bracteoles together below pedicel; pedicel 4–7 mm long (–9 mm in fruit), somewhat thickened distally. Flowers ca 24–28 mm in diameter. Sepals 3.5–5 mm long, 2–2.9 mm wide, the anterior narrower than the lateral 4, all 5 distinct nearly to base, ovate, obtuse or acute at apex, abaxially densely and persistently sericeous with the hairs stramineous except for a narrow marginal white-tomentose zone, adaxially thinly white-sericeous in proximal $\frac{1}{2}$ and glabrous distally, the anterior eglandular or rarely biglandular and $\pm$ erect, the lateral 4 biglandular and strongly incurved or inrolled in anthesis, the glands 2.2–2.8 mm long, 1–1.4 mm wide, elliptical, attached their whole length, slightly separated (i.e., not compressed). Petals orange-yellow, glabrous, fimbriate-laciniate and eglandular or the divisions at base of limb slightly glandular-thickened, the limb of the anterior-lateral 2 bent upward in distal $\frac{1}{2}$ and the limb of the posterior often reflexed in distal $\frac{1}{2}$, all with the claw entire; anterior-lateral petals with the claw 4.5–6 mm long, posterior-lateral petals with the claw 3–3.5 mm long, all 4 lateral petals with the limb oblate or obovate or roughly circular, 7–11 mm long, 8–12 mm wide; posterior petal with the thick claw 3–3.5 mm long, the limb roughly circular except for the broadly cuneate base, 7.5–10 mm long, 7.5–11 mm wide. Stamens 6, 5 opposite sepals plus 1 opposite posterior petal, all fertile; filaments glabrous, the anterior 3 free, the posterior 3 connate in proximal 1–2 mm and swollen at base, all crowded around style and curved downward toward anterior sepal and then upward, the posterior notably shorter than the 5 opposite sepals (anterior 6–7 mm long, anterior-laterals 5.5–6.5 mm long, posterior-laterals 5–6 mm long, posterior 3–4 mm long); anthers alike or subequal, 1–1.5 mm long, densely spreading-tomentose on locules, the connective not or only slightly exceeding locules, sometimes reddish but not enlarged or glandular. Carpels 3, 1 anterior and 2 posterior, hairy; style 1, borne on anterior carpel, 6–7.5 mm long, glabrous, stout, lying in plane of symmetry of flower, curved downward toward anterior sepal and then upward, bent abruptly upward at apex (often nearly 90°), the elliptical stigma displaced to 1 side so that it points outward away from the subtending cluster of 5 longer stamens. Samaras developing with their wings erect and parallel, the anterior samara and 1 posterior with the adaxial edge of the wing pointed in 1 direction and the other posterior samara between them and oriented

at 180° to them, separating from a low rounded torus ca 1.5 mm high; samara ca 20 mm long, sericeous on nut and proximally on wing; dorsal wing ca 17 mm long, 7–8 mm wide, with a rounded projection 1.5–2 mm high at adaxial base; nut ca 2.5 mm high, ca 3.5 mm long, globose, quite smooth on the sides, rounded at the base, without any obvious “rostrum,” the lateral winglets represented by a vestigial horizontal flange ca 1 mm long and wide at base of dorsal wing, conduplicate and only with difficulty distinguishable from the dorsal wing; cartilaginous carpophore well developed and functional, extending from receptacle around base of nut and along apparent base of dorsal wing, actually the vestige of lateral winglets. Chromosome number: $n = 20$ (counted in *Anderson 12334*).

TYPE: BRAZIL. Amazonas: Fortaleza Savanna, Rio Puciari, tributary of Rio Ituxi, 20 km above mouth, 29 Jun 1971 fl/imm fr, *Prance et al. 13770* (INPA, holotype; MG, MICH, NY, isotypes).

PARATYPES: BRAZIL. Amazonas, Mpio Humaitá, on hummocks in periodically flooded savannahs SW of Humaitá along road to Pôrto Velho and W of Humaitá along road to Lábrea, ca 50 m: Apr fl, *Anderson 12334* (INPA, MICH, NY); Jun fl, *Ducke* [RB 35609] (MICH, RB); May fl, *Gottsberger & Morawetz 17–5575* (MICH); May fl, *Janssen & Gemtchujnicov 356* (INPA, MICH) and 390 (INPA); Apr fl, *Monteiro & Ramos 858* (INPA); May fl, *Teixeira et al. 286* (MICH); Jun fl, *Teixeira et al. 1054, 1097, 1278* (all MICH); May fl, *Traill 94* (K). Rondônia, vicinity of Pôrto Velho: May fl, *Black & Cordeiro 52–14468* (IAN); Aug fl/imm fr, *Monteiro* [INPA 50856] (INPA); Aug fl, *Rosa 480* (MICH).

Janusia prancei is named for Ghilleen T. Prance, foremost among modern plant collectors in Amazonian Brazil. Its flowers are bilaterally symmetrical, which excludes a close relationship with the three species treated above and their relatives. The species that seems to be most clearly related to *J. prancei* is *J. mediterranea* (Vell.) W. Anderson; they are especially notable for sharing two derived character-states, samaras that are held erect and oriented parallel to each other and samaras with the nut rounded at the base (“erostrate”). *Janusia mediterranea* differs from *J. prancei* in many characters, including wider and more tomentose leaves with usually glanduliferous petioles, umbels not subtended by glanduliferous bracts, well-developed peduncles, and hairy pink-and-white petals with fimbriate claws. *Janusia mediterranea* is a rather isolated species, and *J. prancei* serves as a valuable link tying it firmly to the rest of the genus.

Malpighia emiliae W. Anderson, sp. nov.

Fig. 12.

Frutex 1–2 m altus, ramulis junioribus velutinis. Foliorum majorum lamina 3–6 (–7) cm longa, 1.6–3 (–4) cm lata, ovata vel elliptica, utrinque pertinaciter velutina vel subtus subsericea. Umbella 2-flora; bracteae 0.5–1.3 mm longae; pedunculus florifer 1–5 mm longus; bracteolae 0.3–0.7 mm longae; pedicellus 6–12 mm longus, vix 0.6 mm diametro superans. Sepala abaxialiter sericea, 8–10-glandulifera. Petala rosea, abaxialiter alata ala 0.8–1.5 mm lata et sericea. Styli 2.8–3 mm longi, $\pm$ recti, subaequales, apice dorsaliter rotundati stigmatibus terminalibus vel parum internis. Fructus pyrena sine alis lateralibus dorsalive.

Shrub 1–2 m tall; young stems velutinous, the hairs V-shaped. Lamina of larger leaves 3–6 (–7) cm long, 1.6–3 (–4) cm wide, 1.5–2.5 times as long as wide, ovate or elliptical, obtuse or rounded at base, sometimes rounded but mostly obtuse, acute, or slightly acuminate at apex, biglandular below near base, persistently velutinous on both sides or subsericeous below with all hairs fine, white, V-shaped with straight arms, those below with the arms longer and often widely spread, approaching subappressed; petiole 2–3 mm long, velutinous; stipules 0.3–1 mm

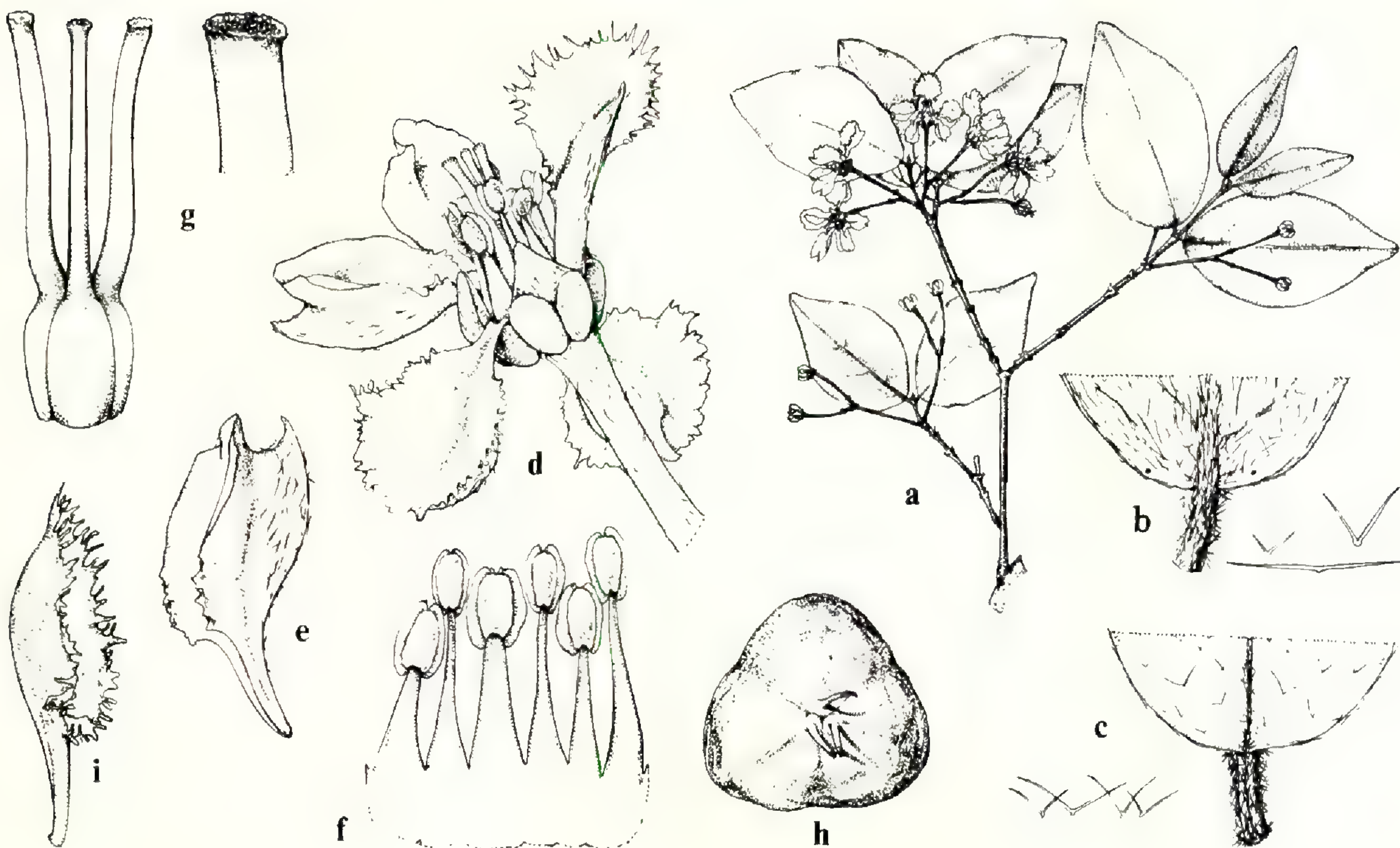


FIG. 12. *Malpighia emiliae* and *M. diversifolia*. a–h, *M. emiliae*: a) habit, $\times 0.5$; b) abaxial surface of lamina, $\times 2.5$, with enlarged hairs, $\times 15$; c) adaxial surface of lamina, $\times 2.5$, with enlarged hairs, $\times 15$; d) flower, side view with posterior petal erect and turned to show its abaxial side, $\times 3.5$; e) lateral petal, side view, $\times 4$; f) partial androecium, laid out, abaxial view, the stamen at left opposite posterior petal, $\times 7.5$; g) gynoecium, anterior style in middle, $\times 7.5$, with apex of 1 style to right, $\times 25$; h) fruit, viewed from above, $\times 1.5$. i, *M. diversifolia*, lateral petal, side view, $\times 4$. Drawn by Karin Douthit, a–g from Lott 1658, h from Lott 1683, i from Brandegee s.n. [UC 187362].

long, distinct, subsericeous. Inflorescence velutinous; umbel raised on a stalk 1–20 mm long, containing 2 flowers; bracts 0.5–1.3 mm long; peduncle 1–5 mm long; bracteoles 0.3–0.7 mm long; pedicel 6–12 mm long, not inflated distally, hardly exceeding 0.6 mm in diameter (dried), velutinous or subsericeous to glabrate. Sepals 1–2 mm long beyond glands, abaxially sericeous, adaxially glabrous, bearing 8–10 glands 1.5–2 mm long, those of the anterior sepal often reduced or partially to completely fused with neighboring glands. Petals pink, all with prominent abaxial wings and loosely sericeous on the wing; lateral petals with the claw 2–2.5 mm long, widening gradually into the limb ca 4.5 mm long and wide, entire distally or erose or dentate proximally or all around the margin, the abaxial wing 1.3–1.5 mm wide, often hookshaped, extending upward nearly or quite as far as apex of limb or even beyond; posterior petal with the claw ca 3.5 mm long, widening gradually into the limb 4.5 mm long and 4.5–5 mm wide, irregularly laciniate, the abaxial wing 0.8–1 mm wide, triangular, only about half as long as limb. Filaments 1.5–3 mm long, $\pm$ straight, connate basally, shortest opposite posterior petal, longest opposite anterior sepal, slightly thicker opposite posterior-lateral petals; anthers 0.8–1.2 mm long, largest opposite posterior-lateral petals, all with swollen connectives. Ovary glabrous, the carpels completely connate; styles 2.8–3 mm long, clearly exceeding anthers in anthesis, slender, straight or the posterior 2 slightly and subtly lyrate, subequal but the anterior usually slightly shorter and slenderer, dorsally rounded at apex with the stigma slightly internal to terminal. Fruit reddish at maturity, 12–14 mm wide and 7–10 mm high (dried), strongly 3-lobed or 3-angled, the pyrenes held in a common flesh at maturity; pyrene endocarp with many fibrous extensions into flesh, but without recognizable lateral or dorsal wings.

TYPE: MEXICO. Jalisco: Mpio La Huerta, Estación de Biología Chamela (UNAM), 19°30'N, 105°03'W, 6.8 km al E de la carretera Barra de Navidad–Puerto Vallarta, viejo camino a Nacastillo, selva baja caducifolia con *Croton*, *Jatropha*, *Coccoloba liebmannii*, *Guapira*, 140 m, 8 Dec 1982 fl, Lott & Wendt 1658 (MICH, holotype).

PARATYPES: MEXICO. Jalisco, Mpio La Huerta, Estación de Biología Chamela (UNAM): Camino Antiguo Sur M 350, deciduous forest, Jun fl, *Bullock 1355* (MICH); same plant as type, Jan fr, *Lott et al. 1683* (MICH); viejo camino a Nacastillo, selva mediana subperennifolia con *Astronium*, *Crataeva*, *Cordia*, *Acalypha*, *Brosimum*, Jan fr, *Lott & Bullock 1687* (MICH); selva baja caducifolia, Aug fl/fr, *Magallanes 3712* (MICH); selva baja caducifolia, con *Ipomoea*, *Plumeria*, Jul fr, *Pérez 1390* (MICH); selva baja caducifolia, en los terrenos planos, Jul fl/fr, *Pérez 1754* (MICH).

Malpighia emiliae is named in honor of Emily J. Lott, in recognition of her fine work on the flora of Chamela. The species is closely related to *M. diversifolia* Brandegees, which is endemic to southernmost Baja California, in habitats somewhat drier but probably not so very different from the deciduous tropical woodlands of Nueva Galicia. In *M. diversifolia* the generally smaller leaves are usually broader relative to their length than in *M. emiliae* (L:W = 1–1.7), with the apex varying from obtuse to rounded or emarginate. However, the most impressive differences are in the petals and pyrenes. The petals of *M. diversifolia* are abaxially smooth or only slightly carinate and glabrous or very sparsely piliferous; compare e and i in Figure 12. The pyrenes bear well-developed lateral and dorsal wings and intermediate outgrowths. I acknowledge with thanks the loan of specimens of *M. diversifolia*, including its type, by the University of California at Berkeley for comparison with *M. emiliae*.

Malpighia novogaliciana W. Anderson, sp. nov.

Fig. 13.

Frutex vel arbor parva 1.5–5 m alta, pilis ramulorum juniorum stipitatis stipitibus persistentibus. Foliorum majorum lamina 5.5–9.5 cm longa, 2.5–4.5 cm lata, apice acuminata acumine 0.8–1.7 cm longo, subtus $\pm$ pertinaciter sericea pilis 1.5–2.7 mm longis, crassis, luteis. Umbella 2–4 (–6)-flora, sessilis vel in pedunculo communi usque ad 2 mm longo elevata. Petala rosea, abaxialiter paulo carinata sericea, 4 lateralibus erosa vel distaliter dentata, posticum profunde dentatum. Filamenta heteromorpha, illa petalis postico-lateralibus opposita crassiora, valde arcuata, 3.5–4.2 mm longa. Styli apice uncis dorsalibus 0.1–0.2 mm longis instructi, 2 postici 3.7–4.5 mm longi, valde arcuati. Fructus luteus vel aurantiacus, minimum 20 mm latus $\times$ 15 mm altus (vivus), indehiscens.

Shrub or small tree 1.5–5 m tall; young stems sericeous, the mostly fine white hairs borne on short, persistent, peglike bases; older stems glabrescent and lenticellate, the peglike hair-bases eventually abraded. Lamina of larger leaves 5.5–9.5 cm long, 2.5–4.5 cm wide, elliptical, cuneate at base, acuminate at apex with the acumen 0.8–1.7 cm long, biglandular below near base; adaxial surface initially loosely sericeous but soon quite glabrate; abaxial surface initially densely sericeous, many of the finer hairs soon deciduous but others thickening and stiffening, becoming stout, stiff, needle-like, yellowish or golden, 1.5–2.7 mm long, persistent, forming a dense to sparse layer over whole surface; petiole 1.5–3 mm long, sericeous to glabrate; stipules 0.5–1.2 mm long, distinct, sericeous to glabrate. Inflorescences axillary to current leaves or borne on older leafless stems, sericeous or subvelutinous; umbel sessile or raised on a stalk up to 2 mm long, containing 2–4 (–6) flowers; bracts and bracteoles 0.5–1 mm long; peduncle 1.5–

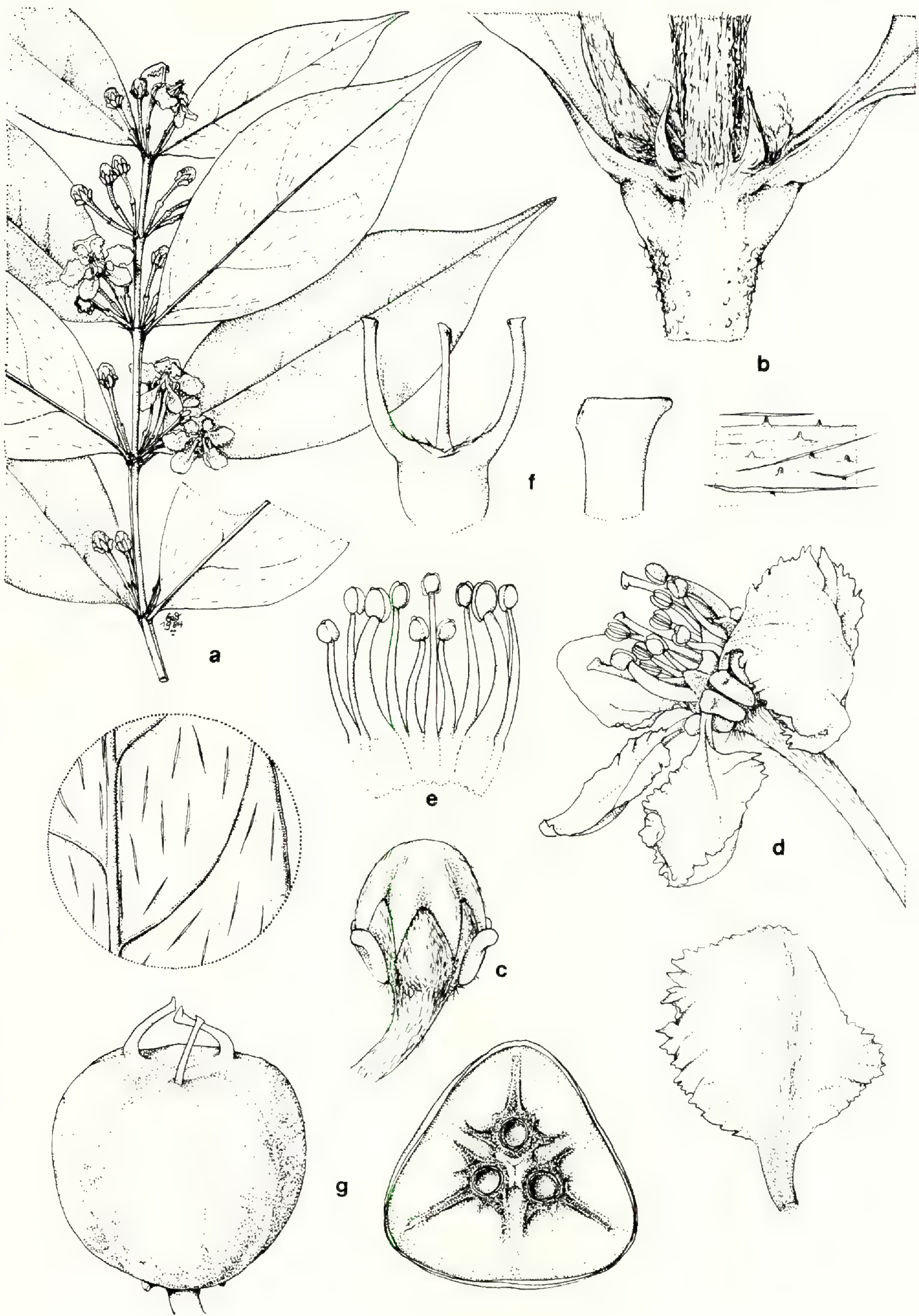


FIG. 13. *Malpighia novogaliciana*. a) habit, $\times 0.7$, with enlargement of abaxial surface of lamina, below, showing needle-like hairs, $\times 2.8$; b) node, showing stipules, $\times 10.5$, with enlargement, below, of stem hairs borne on peglike bases, $\times 28$; c) flower bud, $\times 5$; d) flower, side view with reflexed posterior petal to right, $\times 3.5$, and below a lateral petal, abaxial side, $\times 5$; e) androecium, laid out, abaxial view, the stamen at left opposite posterior petal, $\times 6.5$; f) gynoecium, anterior style in middle, $\times 5$, with apex of 1 style to right, $\times 25$; g) immature fruit, $\times 2.8$, the cross section at right showing developing wings of pyrenes. Drawn by Karin Douthit, a–b from Lott 3824, c–f from Bornstein 89a, g from Bornstein 89b.

6.5 mm long; pedicel 5–8.5 mm long, sericeous to glabrescent. Flowers 1.5–2 cm in diameter. Sepals 0.5–1 mm long beyond glands, triangular, abaxially sericeous, adaxially glabrous, the lateral 4 bearing 6 (–8) glands free at apex, the posterior 6 glands 2–2.5 mm long, the anterior 2, if present, much smaller. Petals pink or “pink and white,” abaxially very slightly carinate with the low keel hardly measurable, sparsely sericeous on and beside keel; lateral petals with the claw 2–2.3 mm long, the limb 4.5–5.5 mm long, 4.1–6 mm wide, often asymmetrical, erose or distally dentate; posterior petal with the claw 3 mm long, the limb 5.5–6 mm long, 7–7.3 mm wide, deeply dentate, somewhat crumpled, strongly reflexed. Filaments heteromorphic, those opposite posterior-lateral petals much thicker than others and strongly bowed, 3.8–4.2 mm long, the other 8 slender and straight or somewhat curved or bowed, shortest opposite the posterior petal (1.8–2.5 mm long), longest opposite the anterior sepal (3.5–4 mm long), 2–3.7 mm long in intermediate positions; anthers 0.6–1.2 mm long, largest on the 2 thicker filaments. Ovary glabrous, the carpels completely connate; styles sparsely sericeous at base, all with distinctly internal stigmas and short dorsal hooks at apex 0.1–0.2 mm long; anterior style 2.7–3.7 mm long, nearly straight, bent slightly toward posterior petal; 2 posterior styles 3.7–4.5 mm long, strongly bowed, horizontal at base and then arched inward and twisted slightly toward posterior petal. Fruit yellow or orange at maturity, at least 20 mm wide and 15 mm high when fresh, probably larger, 18 mm wide and 13 mm high when dried; pyrenes held in a common flesh at maturity; dorsal and lateral wings of pyrene well developed but completely obscured by the thick flesh; styles 7–10 mm apart in fruit.

TYPE: MEXICO. Jalisco: Ca 5 km NW of Río San Nicolás, 20 km SE of Tomatlán, tall lowland forest of *Hura*, *Caesalpinia*, *Guaiaacum*, *Sebastiania*, *Jatropha*, 90–150 m, 11–12 Dec 1970 fr, *McVaugh* 25242 (MICH, holotype; CAS, ENCB, F, MEXU, NY, isotypes).

PARATYPES: MEXICO. Jalisco: Chamela, Mpio La Huerta, selva mediana subperennifolia con *Brosimum*, *Mastichodendron*, *Astronium*, *Lott et al.* 1706, Sep fl, *Magallanes* 3824 (both MICH). Colima: Ca 28 km S of Colima on side road to Ixtlahuacán, 430 m, 6 Jun fl, *Bornstein* 89a (CAS, CHAP, DUKE, GH, INIF, MEXU, MICH, NY), 14 Jun imm fr, *Bornstein* 89b (CAS, CHAP, GH, INIF, MEXU, MICH, NY); ca 25 km SSW of Colima on road to Manzanillo, deciduous woodland dominated by Leguminosae, *Bursera*, *Hura*, 300 m, Jul fr, *McVaugh* 15549 (ENCB, MICH, US); ca 25 km WNW of Santiago on road to Cihuatlán, deciduous forest dominated by Leguminosae, *Bursera*, *Ficus*, sea level to 30 m, Jul fr, *McVaugh* 15737 (ENCB, GH, IBUG, K, MICH, MO).

Malpighia novogaliciana is endemic to the deciduous forests of the Pacific slope in Nueva Galicia. It is most closely related to *M. souzae* Miranda, a species of the tall, wet, mostly evergreen forests of Chiapas, Veracruz, Tabasco, Yucatán, and Belize. Aside from its ecological and geographical distinctness, *M. souzae* differs from *M. novogaliciana* in these characters: Stature up to 15 m; larger leaves with the acuminate apex 1.5–3 cm long; abaxial surface of the lamina initially sericeous but nearly glabrate below at maturity except often thinly sericeous on the midrib, the hairs very fine, white, 0.5–1.3 mm long; petals with a prominent abaxial keel ca 0.2 mm wide; lateral petals erose or fimbriate on the proximal half; posterior petal deeply fimbriate; filaments opposite the posterior-lateral petals 3–3.3 mm long; styles glabrous or with a few basal hairs, bearing apical-dorsal hooks 0.2–0.3 mm long; fruit reported to be 35 mm wide and high when fresh, 17–25 mm when dried.

Malpighia rzedowskii W. Anderson, sp. nov.

Fig. 14.

Frutex vel arbor parva 1–4 m alta, ramulis junioribus velutinis. Foliorum majorum lamina 7–14 (–16.5) cm longa, 4–7 cm lata, apice plerumque acuminata, utrinque pertinaciter velutina, pilis supra V- vel Y-formibus, subtus Y- vel T-formibus. Umbella 4-flora; bracteae 2–6 mm longae; pedunculus florifer 1–3 (–4) mm longus; bracteolae 1–2 mm longae; pedicellus 2–4 mm longus (–5.5 mm in fructu), distaliter 1–1.5 mm diametro. Sepala abaxialiter sericea, 8–10-glandulifera. Petala rosea, abaxialiter carinata carina angusta crassaque, glabra. Styli ca 2 mm longi, recti, subaequales, apice parum inflexi. Fructus pyrena alis lateralibus et dorsali instructa.

Shrub or small tree 1–4 m tall; young stems velutinous, the hairs V- or Y-shaped. Lamina of larger leaves 7–14 (–16.5) cm long, 4–7 cm wide, ovate or elliptical, obtuse at base, mostly acuminate at apex, bearing 0–1 gland below near each margin 10–15 mm above base, persistently velutinous on both sides with all hairs fine and white, those on adaxial surface shorter, V- or Y-shaped, those on abaxial surface Y- or T-shaped, most with the arms nearly or quite straight; petiole 3–5 mm long, velutinous like the stems; stipules 0.5–1.5 mm long, distinct, subsericeous to glabrate. Inflorescence velutinous like the stems; umbel raised on a stalk 7–13 mm long, containing 4 flowers; bracts 2–6 mm long; peduncle 1–3 (–4) mm long; bracteoles 1–2 mm long; pedicel 2–4 mm long (–5.5 mm in fruit), distally swollen, 1–1.5 mm in diameter, subvelutinous to subsericeous. Sepals ca 1 mm long beyond glands, abaxially sericeous, adaxially glabrous, bearing 8–10 glands 1.5–2.8 mm long, often with partial to complete fusion of 1 or 2 pairs of neighboring glands on the anterior 3 sepals. Petals pink, abaxially carinate with the low thick inconspicuous keel not reaching apex of petal, glabrous; lateral petals with the claw 1.5–2 mm long, the limb 3–4 mm long, 2.5–4 mm wide, often asymmetrical, distally entire or denticulate, proximally dentate to lacinate; posterior petal with the claw 2 mm long, the limb 3.5–4.5 mm long, 6–7 mm wide (spread flat), lacinate. Filaments 2–2.8 mm long, straight, connate basally, subequal in thickness or the 2 opposite posterior-lateral petals slightly thicker; anthers 0.9–1.2 mm long, longest opposite posterior-lateral petals. Ovary glabrous or bearing a few hairs distally, the carpels completely connate; styles ca 2 mm long, not or hardly exceeding anthers in anthesis, straight, alike or the anterior slightly shorter, slightly inbent at apex, the stigma internal or appearing nearly terminal. Fruit red and glabrous at maturity, “2.5 cm diam.” (McVaugh 16037) when fresh, 15 mm wide and 12–13 mm high when dried, the pyrenes held in a common flesh at maturity; pyrene with well-developed lateral wings and narrower dorsal wing and intermediate winglets, all visible in dried fruit.

TYPE: MEXICO. Jalisco: Mpio La Huerta, 2 km al NW de Chamela, orilla de una laguna costera salobre con vegetación de mangle y otras plantas, 28 Aug 1976 fl, *Rzedowski & McVaugh 1409* (MICH, holotype; ENCB, MEXU, isotypes).

PARATYPES: MEXICO. Jalisco: Mpio La Huerta, Los Angeles Locos de Tenacatita, 4 km de la carretera Barra de Navidad–Puerto Vallarta, selva baja caducifolia perturbada con *Acalypha*, *Croton*, *Jatropha*, Oct fr, *Lott 1377* (MICH). Colima: Mountain summits near pass ca 18 km SSW of Colima on Manzanillo road, deciduous woodland now nearly in full foliage, dominated by various Leguminosae, *Bursera*, *Cnidoscolus*, 500 m, Aug fr, *McVaugh 16037* (CAS, ENCB, MEXU, MICH, MO, NY).

Malpighia rzedowskii is named for Jerzy Rzedowski, in recognition of his many contributions to Mexican botany. It is most closely related to *M. mexicana* Adr. Juss., in which the umbel usually contains more flowers (4–8 or more,

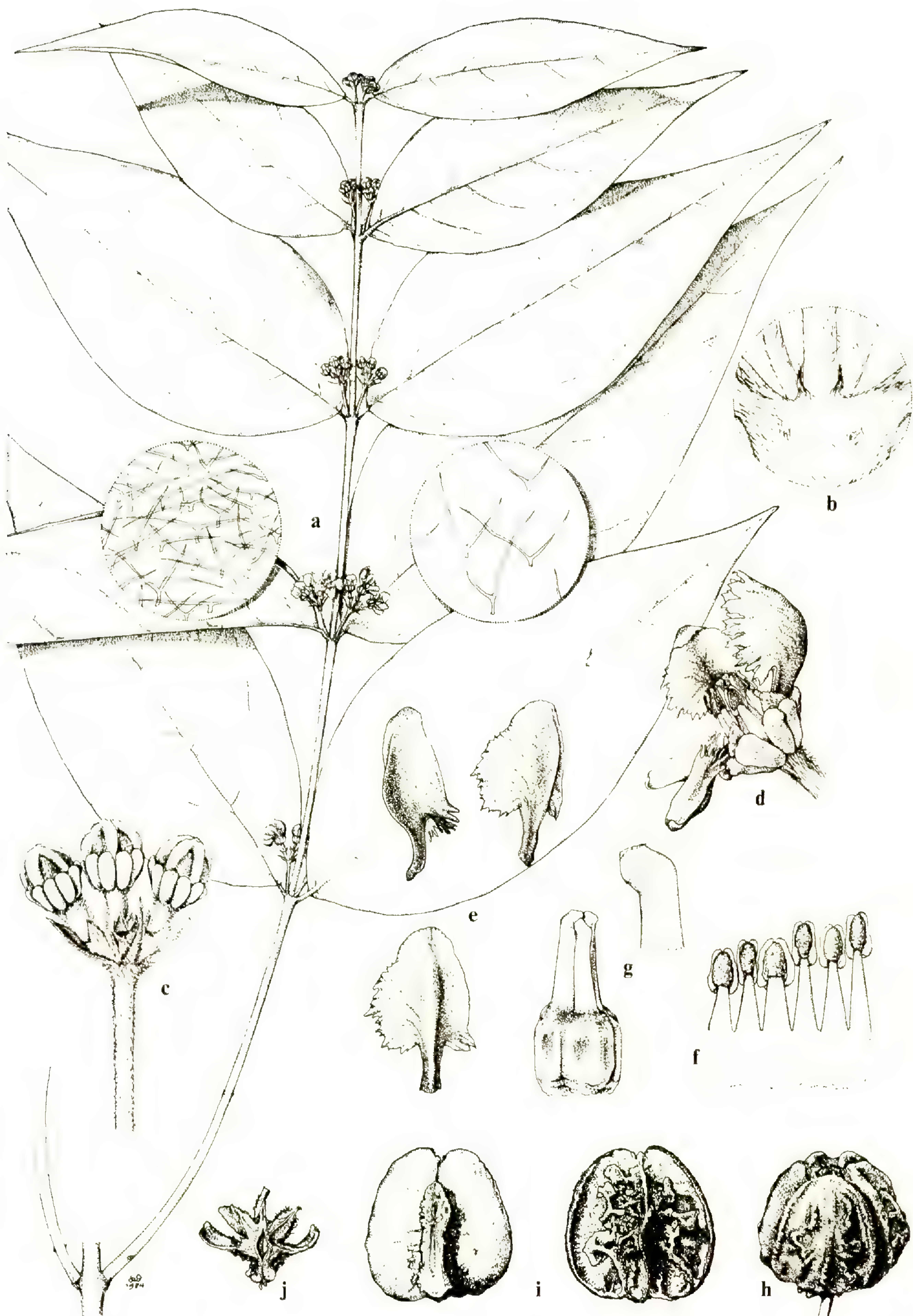


FIG. 14. *Malpighia rzedowskii*. a) habit, $\times 0.5$, with enlarged hairs from both surfaces of lamina, $\times 25$, abaxial to left, adaxial to right; b) node, showing stipules, $\times 5$; c) umbel of flower buds, with 1 removed, $\times 2.5$; d) flower, side view with posterior petal erect and 1 posterior-lateral petal removed, $\times 3$; e) petals, $\times 4$, above left an anterior-lateral petal, above right and below 2 posterior-lateral petals; f) partial androecium, laid out, abaxial view, the stamen at left opposite posterior petal, $\times 6$; g) gynoecium, anterior style in middle, $\times 6$, with apex of 1 style above, $\times 10$; h) fruit, dried but intact, $\times 1.5$; i) 1 pyrene of fruit with flesh removed, adaxial side left, abaxial side right, $\times 1.5$; j) cross section of 1 pyrene of fruit with flesh removed, $\times 1.5$. Drawn by Karin Douthit, a–g from *Rzedowski & McVaugh 1409*, h–j from *McVaugh 16037*.

commonly at least 6) and the pedicel is longer and not inflated. The most dramatic difference lies in the hairs of the leaves, stems, and inflorescence, which are strongly twisted in *M. mexicana*, producing a tomentose vesture.

***Malpighia stevensii* W. Anderson, sp. nov.**

Fig. 15.

Frutex vel arbor parva 2–8 m alta, ramulis dense tomentosis. Folia nunc in ramis lateralibus brevissimis conferta, nunc in ramis elongatis portata; foliorum majorum lamina 3–8.5 (–9.5) cm longa, 2–6 (–7.5) cm lata, elliptica, subrotunda, vel saepius obovata, apice obtusa vel rotundata, subtus basi margine 2–4-glandulifera, supra tomentosa mox vel demum glabrata, subtus pertinaciter tomentosa. Umbella 2–4-flora, in pedunculo communi 0.5–5 (–12) mm longo elevata. Petala rosea. Stamina heteromorpha, illa petalis postico-lateralibus opposita filamentis crassioribus et antheris majoribus. Ovarium plerumque dense pilosum, interdum glabrum; styli apice apiculati, 2 postici e basi arcuati. Fructus 13–20 mm latus, 9–15 mm altus.

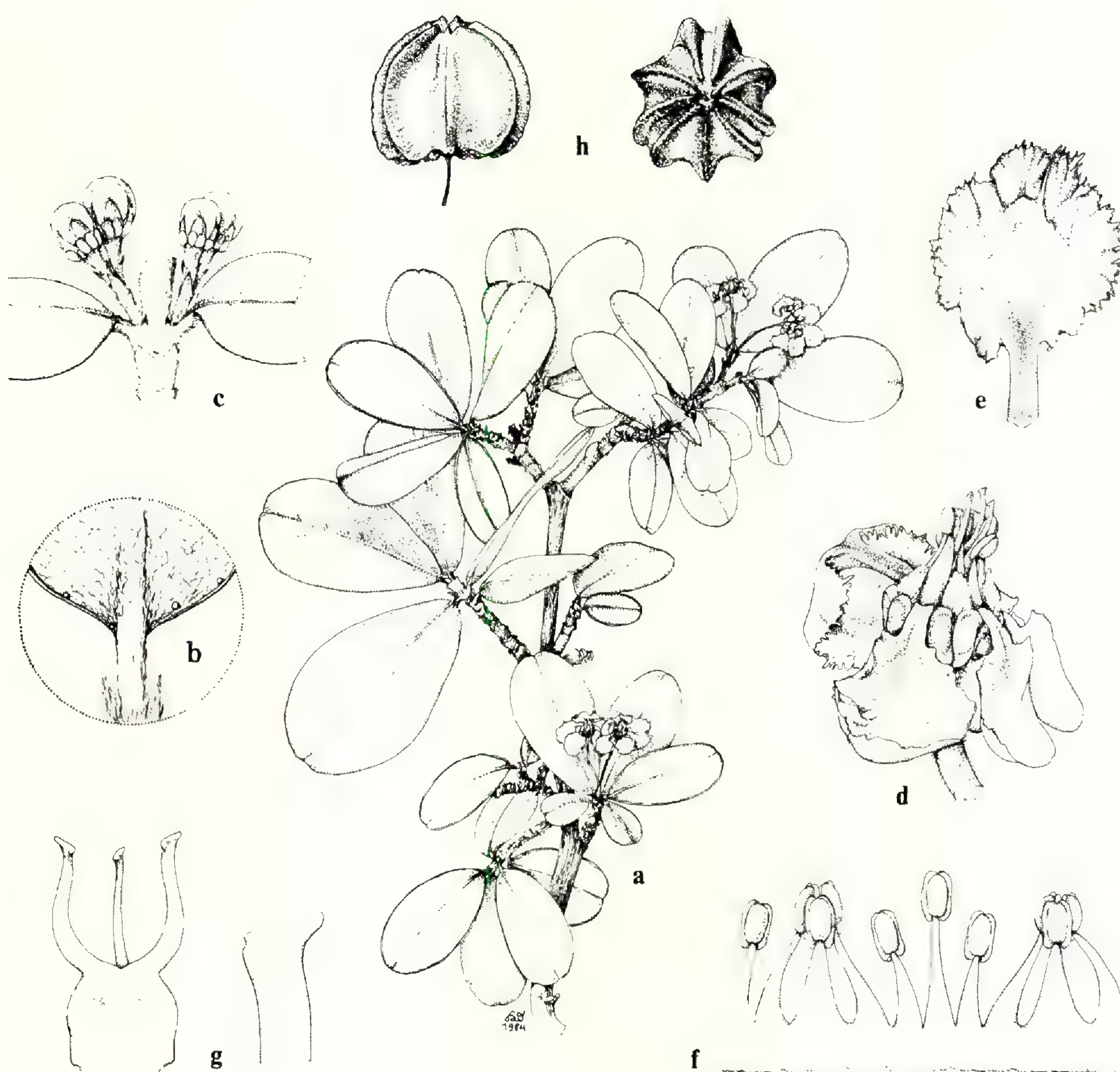


FIG. 15. *Malpighia stevensii*. a, flowering branch, $\times 0.5$; b, base of leaf and stipules, abaxial side, $\times 3$; c) axillary 2-flowered umbels, $\times 1$; d) flower, side view, posterior petal to left, $\times 3$; e) posterior petal, flattened, $\times 3$; f) androecium, laid flat, abaxial view, the stamen to left opposite posterior petal, $\times 5$; g) gynoecium, anterior style in middle, $\times 5$, with apex of 1 style to right, $\times 20$; h) dried fruit, side view (left) and from above (right), both $\times 1$. Drawn by Karin Douthit, a from *Stevens 14675*, b–g from *Stevens 22927*, h from *Stevens 9123*.

Shrub or small tree 2–8 m tall; stems initially densely tomentose, eventually glabrate. Some leaves usually borne on short lateral shoots on old stems, with little or no internode between successive pairs, the same plants also bearing stems with well-developed internodes; lamina of larger leaves 3–8.5 (–9.5) cm long, 2–6 (–7.5) cm wide, elliptical, subrotund, or most often obovate, broadly cuneate or rounded at base, obtuse or rounded and often apiculate or emarginate at apex, bearing 2–4 glands below at base on or by margin, densely tomentose on both sides initially, soon or eventually glabrate above, persistently tomentose below or belatedly glabrescent; petiole 2–5 mm long, tomentose to glabrate; stipules 0.5–1.5 mm long, distinct. Inflorescence tomentose or subsericeous; umbel raised on a stalk 0.5–5 (–12) mm long, containing 2–4 flowers; bracts 0.7–1.5 mm long; peduncle 1–5 mm long; bracteoles 0.5–1 mm long; pedicel 6–9 mm long, appressed-tomentose. Sepals 1–1.5 mm long beyond glands, abaxially uniformly appressed-tomentose, adaxially glabrous, bearing 6–10 glands, the posterior 6 2–2.8 mm long, the anterior 1–4, if present, usually smaller. Petals pink, abaxially smooth or keeled on claw and lower limb, sparsely sericeous or glabrous; lateral petals with the claw 2–3 mm long, the limb (4–) 5–6 mm long, 5–6.5 (–7.5) mm wide, irregularly shaped and often asymmetrical, entire or somewhat erose; posterior petal with the claw 2.5–3 mm long, the limb erect to strongly reflexed, 6–8 mm long and wide, orbicular, puckered toward margin, erose or dentate. Stamens heteromorphic, those opposite posterior-lateral petals with thicker filaments and somewhat larger anthers than others; filaments 2–3.5 mm long, basally connate; anthers 1–1.5 mm long. Ovary usually densely hairy, occasionally glabrous, the carpels completely connate; styles with distinctly internal stigmas, usually apiculate dorsally at apex, rarely truncate; anterior style 2.2–2.5 mm long, slenderer than posterior ones, $\pm$ straight and erect or leaning slightly backward; 2 posterior styles ca 2.5–3 mm long, bowed outward from base, then ascending. Fruit “pink” or “orange” at maturity, sparsely tomentose or glabrous, 13–20 mm wide, 9–15 mm high, the pyrenes firmly united and held in a common flesh at maturity; pyrene with well-developed dorsal and lateral wings and several intermediate outgrowths, all obscured by the flesh.

TYPE: NICARAGUA. Estelí: Km 163 on Hwy 1, ca 11.2 km N of entrance to Estelí, 13°13'N, 86°23'W, 920 m, level rocky plain on old basalt, thorn scrub with cacti and *Agave* conspicuous, 29 Jun 1978 fr, *Stevens 9123* (MICH, holotype).

PARATYPES: NICARAGUA. Estelí: Llano de Santa Adelaida, 13°14'N, 86°22'W, ca 850 m, Jan fl, *Moreno 14095* (MO), Apr fl, *Moreno 16154* (MO), Dec fl/fr, *Moreno 25144* (MICH); type locality, Sep fl, *Stevens 23124* (MO). León: Río El Tamarindo, bosque de galería, suelo rocoso, Oct fr, *Grijalva et al. 3053* (MICH); camino a El Velero, 4.3 km de la carretera a Puerto Sandino, 20 m, Feb fl, *Moreno 6525* (MO); La Paz Centro, 12°15'N, 86°43'W, 60 m, Jun fl, *Moreno 24248* (MICH); Hwy 12, 12°15'N, 86°43'W, 30 m, rocky savanna, Dec fr, *Stevens 11183* (MICH), Oct fl, *Stevens 14675* (MICH, MO); El Velero, at mouth of Estero San José, 12°08'N, 86°45'W, mangrove margin, Sep ster, *Stevens 23081* (MICH). Matagalpa: camino de “Puertas Viejas,” 12°36–38'N, 86°03–04'W, 500–600 m, Sep fl, *Araquistain 3665* (MO); Puertas Viejas, 1–2 km camino a San José de los Remates, 430–470 m, May fl/fr, *Moreno 16229* (MICH), Nov fr, *Moreno 18308* (MICH); Quebrada Santa Cruz, between Puertas Viejas and Esquipulas, 420 m, Jul fl, *Stevens 22346* (MICH). Managua: Rancho Grande, al N de Río Pacora, 12°27–29'N, 86°11–13'W, 80–90 m, bosque tropical muy seco, caducifolio, May fr, *Araquistain 3510* (MICH); Las Maderas, “Las Pilas” y “El Platanal,” 12°27'N, 86°04'W, 60–80 m, Nov fr, *Moreno 18705* (MICH); La Mojarra, 12°35'N, 86°21'W, 60–80 m, Jun fl, *Moreno 21433* (MICH); Km 64, 1 km al W del caserío “El Madroño,” 12°32'N, 86°04'W, 500 m, Dec fl/fr, *Moreno 22544* (MO). Boaco: 4 km al S de Boaquito, 12°26'N, 85°44'W, 200 m, Oct fr, *Moreno 18051* (MICH); 2 km al N de Boaquito, 300 m, Oct fr, *Moreno 18097B* (MO); 1 km al E de Santa Cruz, 12°24'N, 85°49'W, 200 m, Nov fl, *Moreno 22467A* (MICH); Finca San Antonio, 9 km al SW de Boaco,

12°26'N, 85°44'W, 200 m, Jul fl/fr, *Moreno 24341* (MICH), Sep fl/fr, *Moreno 24793* (MO); 3 km N of Tecolostote, along Río San Lorenzo, 12°16'N, 85°39'W, 120 m, gallery forest, Jan fl, *Stevens 22927* (MICH). Granada: Isla Zapatera, Cerro El Llano (falda norte), 100 m, bosque seco tropical, Aug fr, *Grijalva 821* (MICH). Chontales: Km 82 de la carretera al Rama, 12°15'N, 85°39'W, 120–200 m, Nov fl, *Moreno 18691* (MO).—COSTA RICA. Guanacaste: 28 km N of Cañas, 100 m, dry forest, Oct fl, *Frankie 312 C* (F); El Coco, Carrillo, en pendientes rocosas al borde de la playa, Aug fl, *Jiménez M. 980* (F, NY).

This species is named for Warren Douglas Stevens, who has made a superb contribution to our knowledge of the plants of Nicaragua. *Malpighia stevensii* is closely related to *M. emarginata* DC., which differs most notably in having the stems and leaves sparsely sericeous to glabrate; also, its leaves are usually narrower, the leaf glands are usually only 2 and set in from the margin, and its ovary is usually glabrous.

***Malpighia verruculosa* W. Anderson, sp. nov.**

Frutex 1–3.5 m altus, pilis ramulorum hornotinorum stipitatis stipitibus persistentibus. Foliorum majorum lamina 4–6.5 (–7.5) cm longa, 2–3.2 cm lata, elliptica, apice plerumque acuminata, subtus pertinaciter sparsim sericea pilis 1.5–2.5 mm longis, crassis, luteis. Umbella (1–) 2 (–3)-flora. Petala rosea, anguste carinata, glabra vel paucipilifera. Stamina heteromorpha, illa petalis postico-lateralibus opposita filamentis crassioribus et antheris majoribus. Styli postici ca 3 mm longi, e basi arcuati, apice apiculati. Fructus dehiscens.

Shrub 1–3.5 m tall; young stems initially subsericeous or subhispid with the short stiff hairs borne on persistent, thickened, peglike bases up to 0.2 mm long, the hairs soon deciduous, the bases eventually abraded from older stems. Leaves evenly spaced, successive pairs separated by internodes; lamina of larger leaves 4–6.5 (–7.5) cm long, 2–3.2 cm wide, elliptical, cuneate or rounded at base, acuminate or rarely acute at apex, biglandular below near base, soon glabrate above, thinly but persistently sericeous below with the longer hairs 1.5–2.5 mm long, stout, yellow, sessile, straight, strongly appressed, parallel to midrib; petiole 1–2 mm long, sericeous to glabrate; stipules 0.5–1.5 mm long, distinct. Inflorescence thinly sericeous to glabrate; umbel raised on a stalk (2–) 4–11 (–15) mm long, containing (1–) 2 (–3) flowers; bracts 0.8–1.3 mm long; peduncle 3–6 mm long; bracteoles 0.6–1 mm long; pedicel 6–13 mm long, soon glabrate. Sepals ca 2.5 mm long, bearing a few hairs abaxially, glabrous adaxially, the lateral 4 bearing 6 (–7) glands 2 mm long. Petals pink, abaxially narrowly keeled, glabrous or very sparsely pilose; lateral petals with the claw 1.5–2 mm long, the limb 5–6 mm long, 4–6 mm wide, somewhat conduplicate, erose; posterior petal with the claw 3 mm long, the limb 6 mm long, 7.5 mm wide, flat, coarsely toothed or laciniate. Stamens strongly heteromorphic, those opposite posterior-lateral petals with much thicker filaments and larger anthers than others; filaments 1–3 mm long, basally connate; anthers 0.8–1.7 mm long. Ovary glabrous, the carpels connate only along shared ventral faces; styles with distinctly internal stigmas; anterior style ca 2.3 mm long, slenderer than posterior styles, slightly curved toward posterior petal, truncate at apex; 2 posterior styles ca 3 mm long, strongly bowed outward from base, then ascending, dorsally apiculate at apex. Fruit red at maturity, the pyrenes joined only along a narrow ventral areole 3–5 mm long, breaking apart at maturity; pyrene 1.1–1.5 cm long (dried), with well-developed dorsal and lateral winglets and an intermediate crest on each side.

TYPE: NICARAGUA. Rivas: Slopes of Volcán Maderas above coffee plantations above Balgüe, Isla de Ometepe, 11°28'N, 85°31'W, 600–800 m, cloud forest-rain forest, 14 Sep 1983 fl/fr, *Nee & Téllez 28038* (MICH, holotype).

PARATYPES: HONDURAS. Colón: Tropical forest, Guarunta, Wispemini Camp, 15–25 m, Mar fr, *von Hagen & von Hagen 1405* (F).—NICARAGUA. Zelaya: El Naranjo, carretera Waslala a Siuna, 13°34'N, 85°11'W, 280–300 m, Dec fr, *Moreno 19169* (MO); montañas y bosques lluviosos entre Toro Bay y Esquipulas, drenajes de los Ríos Júcaro y Esquipulas, 130 m, Nov fr, *Shank & Molina 4617 & 4681* (both F); bosque lluvioso de montañas de Esquipulas y Alemán, drenaje de Río Alemán, 150 m, Nov fr, *Shank & Molina 4768, 4781, 4816 & 4881* (all F); matorrales y potreros húmedos, drenajes de los Ríos Punta Gorda, Alemán y Zapote, 30 m, Dec fr, *Shank & Molina 4981* (F). Matagalpa: 78 km de Matagalpa, sobre la carretera Matagalpa–Siuna, La Gloria, 13°15'N, 85°35'W, 600 m, Sep fr, *Moreno 17202* (MICH). Rivas, Isla Ometepe, Volcán Maderas: Faldas del lado N del Volcán, 900–1200 m, Jan fr, *Moreno 19695* (MICH); camino de descenso de la laguna hacia la hacienda Magdalena, bosque húmedo, de lluvia constante, 800–1200 m, Sep fr, *Robleto 1172* (MICH); falda W del Volcán, 700–900 m, Jul fr, *Sandino 952* (MICH).—COSTA RICA. Guanacaste: Heavily forested northern slopes of Volcán Orosí along lower reaches of broad ridge running to N at 650 m, Jan fr, *Wilbur & Stone 9751* (DUKE, F).

Malpighia verruculosa is closely related to *M. albiflora* (Cuatr.) Cuatr., which grows in wet forests from Nicaragua to Colombia. In *M. albiflora* the stem hairs are not borne on persistent bases, the leaf hairs are short, fine, white, and mostly soon deciduous, the umbels usually contain 4–6 flowers, and the petals are white. *Malpighia verruculosa* seems to agree well with the protologue of *M. albiflora* subsp. *antillana* Vivaldi, *Brittonia* 36: 330. 1984, and may be the same taxon. However, Vivaldi has seen eight of the paratypes cited above and in 1980 annotated them as *M. albiflora* subsp. *albiflora*, so apparently he reserves the name *antillana* for specimens from Cuba and Hispaniola. In any case, there are clearly two recognizable taxa in Nicaragua, which I feel should both be treated as species, and since I am uncertain of the correct application of Vivaldi's name I am giving the Central American plants a name at the level of species. If the plants of Cuba and Hispaniola are conspecific with those of Central America, they will have to be called *M. verruculosa*, too. The epithet refers to the dense layer of persistent peglike hair-bases on the young stems, which differentiate the species immediately from all other Central American species of *Malpighia*.

The fruits of *Malpighia albiflora* and *M. verruculosa* give dramatic support to the hypothesis that *Malpighia* is derived from some element in *Mascagnia* through reduction of the samara wings and elaboration of a fleshy exocarp. The pyrenes in these two species are joined only along a narrow ventral areole, like the samaras of *Mascagnia*, and separate at maturity. Beneath their thin flesh the endocarp extends into dorsal and lateral winglets clearly homologous with the wings of a samara in *Mascagnia*.

***Malpighia wendtii* W. Anderson, sp. nov.**

Fig. 16.

Frutex vel arbor usque ad 24 m alta, ramulis glabris mox multis lenticellis instructis. Foliorum majorum lamina 7–10.5 cm longa, 2.5–4.5 cm lata, elliptica, apice acuminata, subtus utrinque in tertio medio 0–2 (–3)-glandulifera, glabra; stipulae distinctae. Umbella (4–) 6–8 (–10)-flora, sparsim sericea mox glabrata, in pedunculo communi 2–5 mm longo elevata. Sepala glabra. Petala alba, laevia, glabra. Stamina heteromorpha, illa petalis postico-lateralibus opposita filamentis crassioribus et antheris majoribus. Ovarium glabrum; 2 styli postici leviter curvati demum valde arcuati, apice uncinati. Fructus ca 16 mm latus, 11–13 mm altus, indehiscens.

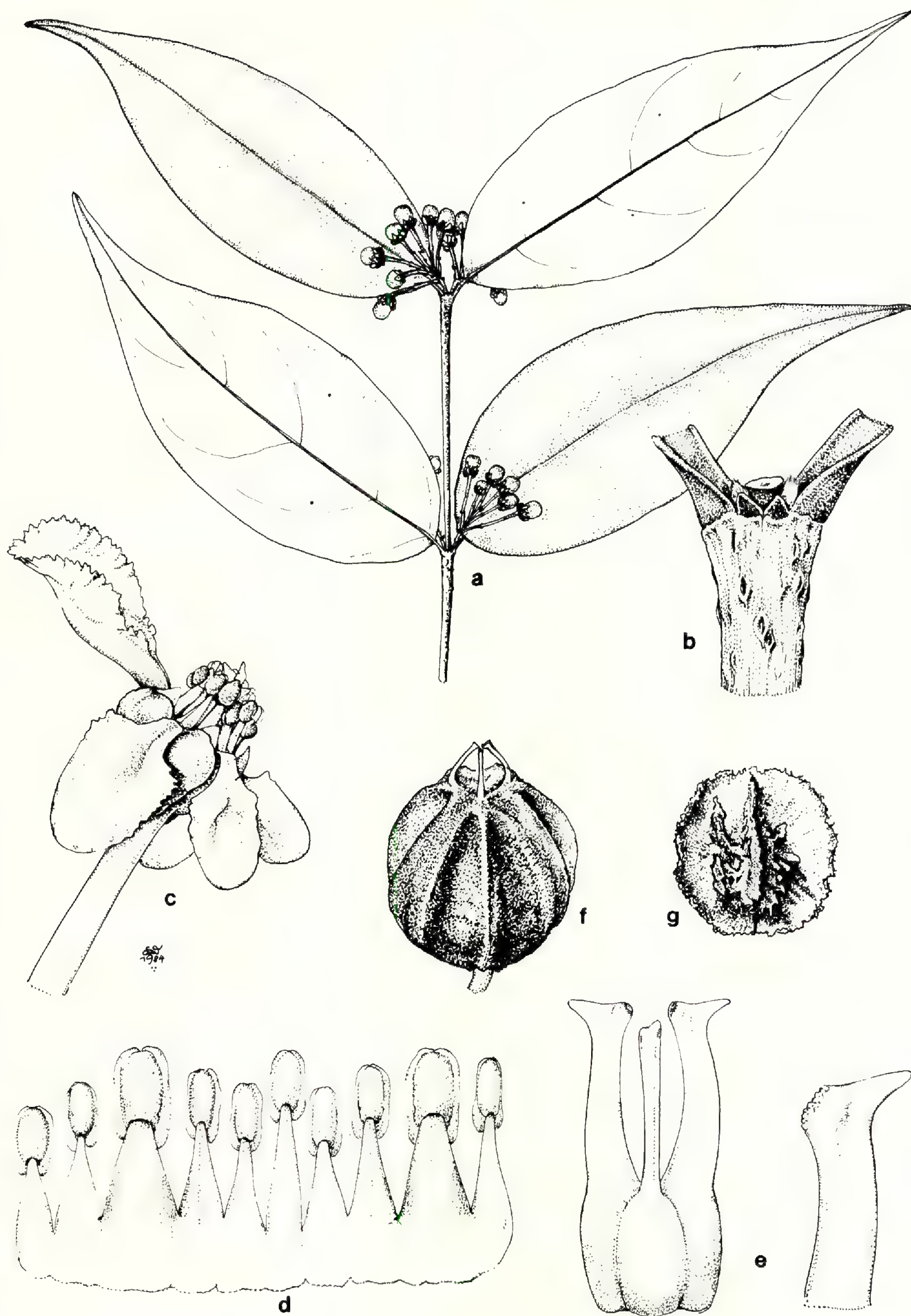


FIG. 16. *Malpighia wendtii*. a) flowering stem, $\times 0.7$; b) node, showing stipules and lenticels, $\times 7$; c) flower, side view, with posterior petal erect, $\times 5$; d) androecium, laid out, abaxial view, the stamen at left opposite posterior petal, $\times 9$; e) gynoecium, anterior style in middle, $\times 10.5$, with apex of 1 lateral style to right, $\times 17.5$; f) fruit, dried but intact, $\times 1.75$; g) 1 pyrene of fruit with flesh removed, abaxial view, $\times 1.75$. Drawn by Karin Douthit, a and c-e from *Wendt* 2825, b, f, g from *Contreras* 7823.

Shrub or tree 2–24 m tall; stems glabrous, soon marked by many raised elliptical lenticels. Leaves evenly spaced, successive pairs separated by internodes; lamina of larger leaves 7–10.5 cm long, 2.5–4.8 cm wide, elliptical or slightly ovate, cuneate or rounded at base, long-acuminate at apex, bearing 0–2 (–3) glands below on each side well above base, $\frac{1}{3}$ – $\frac{1}{2}$ of distance to apex, midway between margin and midrib, glabrous; petiole 3–6 mm long, glabrous; stipules 0.5–0.8 mm long, adjacent but distinct, often reflexed, persistent or deciduous. Inflorescence very sparsely sericeous to glabrate; umbel raised on a stalk 2–5 mm long, usually with a pair of sterile bracts at or below the middle, containing (4–) 6–8 (–10) flowers; bracts and bracteoles 0.5–1 mm long; peduncle 1.5–4.5 mm long; pedicel 6–7 mm long, –10 mm in fruit. Sepals 0.5–1.5 mm long beyond glands, rounded, glabrous, the lateral 4 bearing 6 glands 2.5–3.8 mm long. Petals white, abaxially smooth, glabrous; lateral petals with the claw 1.5–2 mm long, the limb 3–3.5 mm long and wide, entire or denticulate at base; posterior petal with the claw 1.5 mm long, the limb 4.5 mm long and wide, dentate all around margin. Stamens heteromorphic, those opposite posterior-lateral petals with thicker filaments and somewhat larger anthers than others; filaments 2–3 mm long, basally connate; anthers 1–1.5 mm long. Ovary glabrous, the carpels completely connate; styles with distinctly internal stigmas; anterior style 2 mm long, slenderer than posterior ones, straight and leaning forward between posterior styles, apiculate dorsally at apex; 2 posterior styles 2.2–2.3 mm long, initially only slightly bowed but becoming strongly so in old flowers and fruits, prominently hooked dorsally at apex. Fruit probably red at maturity, ca 16 mm wide, 11–13 mm high, the pyrenes held in a common flesh at maturity; pyrene with well-developed dorsal and lateral wings and several intermediate outgrowths, all obscured by the flesh.

TYPE: MEXICO. Veracruz: “Zona Uxpanapa,” Mpio Minatitlán, 17°14'N, 94°18'W, orillas de arroyo estacional de agua mansa, lomas al S del Poblado 11 y al S de la brecha 105, $\pm$ 27 km al E de La Laguna, zona caliza con selva perennifolia, 300 m, 3 Oct 1980 fl, *Wendt, Villalobos, Lott & Navarrete* 2825 (MICH, holotype; CHAPA, isotype).

PARATYPES: MEXICO. Chiapas: Mpio La Trinitaria, montane rain forest 10 km ENE of Dos Lagos above Santa Elena, 1170 m, Aug fr, *Breedlove* 52307 (MICH).—GUATEMALA. Alta Verapaz: Chahal, low forest bordering Seamay River, Oct fr, *Contreras* 7823 (MICH); Chahal, high forest, top of hill, Oct fr, *Contreras* 7851 (MICH). Petén, La Cumbre: High forest on Cadenas Road, Jul fr, *Contreras* 8788 (MICH); high forest on Pusila Road, 1.5 km E of Km 138 of Cadenas Road, Aug fr, *Contreras* 8841 (MICH); high forest 1.5 km W of Km 136/137 of Cadenas Road, Aug fr, *Contreras* 8871 (CHAPA); in *zapotal* on hillside, 1.5 km E of Km 138 of the road, Sep fr, *Contreras* 20305 (MICH).

Malpighia wendtii is named in honor of Thomas L. Wendt, whose work in the Zona Uxpanapa has added many interesting plants to the known flora of Mexico. It is superficially similar to *M. glabra* L., which has pink petals, straight truncate styles, and a smaller fruit without well-developed lateral wings on the pyrenes. Its closest relatives are probably *M. albiflora* (Cuatr.) Cuatr., *M. romeroana* Cuatr., and *M. souzae* Miranda. *M. albiflora* has the carpels only basally coherent in flower and the pyrenes of the fruit separating at maturity. *M. romeroana* has the stipules connate in interpetiolar pairs, a many-flowered inflorescence raised on a stalk at least 12 mm long, and pink petals. In *M. souzae* the stem hairs are borne on persistent peglike bases, the inflorescence contains (2–) 4 flowers, the sepals are hairy, the petals are pink, and the pyrenes do not have such well-developed lateral wings. Although *M. wendtii* may be a shrub or small tree, most collections

have been described as trees 13–24 m tall, which is unusually large for the genus. The species is also notable for its truly glabrous stems and leaves; even *M. glabra* has the stems, and often the leaves, at least initially sparsely sericeous. Most species of *Malpighia* have the leaf glands borne near the base of the lamina, but here they are usually nearer the center, if any are present.

***Malpighia wilburiorum* W. Anderson, sp. nov.**

Fig. 17.

Arbor ca 10 m alta, pilis ramulorum juniorum stipitatis stipitibus persistentibus. Foliorum majorum lamina 7.5–9 cm longa, 2.4–3.2 cm lata, anguste elliptica, apice gradatim angustata vel acuminata, subtus margine pilis 0.7–1.7 mm longis, crassis, luteis instructa. Umbella 4 (–6)-flora, in pedunculo communi (10–) 15–21 mm longo elevata. Sepala abaxialiter sericea, 10-glandulifera. Petala alba vel rosea, abaxialiter paulo carinata sparsissime sericea. Styli $\pm$ recti, apice truncati vel dorsaliter apiculati.

Tree ca 10 m tall, the trunk 20 cm in diameter; young stems initially sericeous with the hairs borne on thickened peglike bases, the hairs soon deciduous, the bases elongating and persistent, eventually abraded from older stems. Leaves evenly spaced, successive pairs separated by internodes 2.5–5 cm long; lamina of larger leaves 7.5–9 cm long, 2.4–3.2 cm wide, narrowly elliptical, obtuse or rounded at base, gradually tapered or acuminate at apex, biglandular below near base, sparsely sericeous to glabrate above with the hairs thin and white, sparsely sericeous to glabrate below, the margin bearing a row of stout, stiff, needle-like, yellowish hairs 0.7–1.7 mm long, these eventually deciduous; petiole 2–2.5 mm long, sericeous to glabrate; stipules 0.8–1.5 mm long, distinct, sericeous to glabrate. Inflorescence sparsely sericeous to glabrate; umbel raised on a stalk (10–) 15–21 mm long, containing 4 (–6) flowers; bracts and bracteoles 0.8–1 mm long; peduncle 3.5–6 mm long; pedicel 6–9 mm long. Sepals 1–1.3 mm long beyond glands, abaxially sericeous, adaxially glabrous, bearing 10 greenish glands 0.8–1.9 mm long, longest on the posterior 3 sepals. Petals “white or pinkish,” abaxially very slightly carinate with the low keel hardly measurable, very sparsely sericeous on keel; lateral petals with the claw 2 mm long, the limb 2.5–3.5 mm long, 2.5–4.5 mm wide, often asymmetrical, entire or erose to lacinate in proximal $\frac{1}{2}$; posterior petal with the claw 4 mm long, the limb 4 mm long, 5 mm wide, lacinate. Filaments 2–2.5 mm long, straight, connate basally, those opposite posterior-lateral petals somewhat thicker than others; anthers 0.7–1 mm long, longest on thicker filaments. Ovary glabrous or bearing a few hairs at apex, the carpels completely connate; styles 1.8–2 mm long, $\pm$ straight, parallel or divergent distally, $\pm$ alike in thickness and length or the anterior slightly slenderer or shorter, truncate at apex or dorsally apiculate, the stigma internal or appearing nearly terminal. Fruit known only from very immature stages.

TYPE: MEXICO. Jalisco: Ca 22 km SSW of Autlán toward La Resolana, open oak woods dominating slopes, 12 Aug 1949 fl, R. L. & C. R. Wilbur 2290 (MICH, holotype; MEXU, isotype).

This species, known only from the type, is named for the brothers Wilbur, who collected it when Robert L. Wilbur was a doctoral student at the University of Michigan. It bears a superficial resemblance to *M. novogaliciana*, because they have somewhat similar leaves, leaf hairs, and peg-based stem hairs. However, the umbel of *M. novogaliciana* is sessile or subsessile, and its posterior styles are strongly bowed, which indicates that the two species are not very closely related. The straight styles indicate a general relationship with *M. glabra* L., a shorter

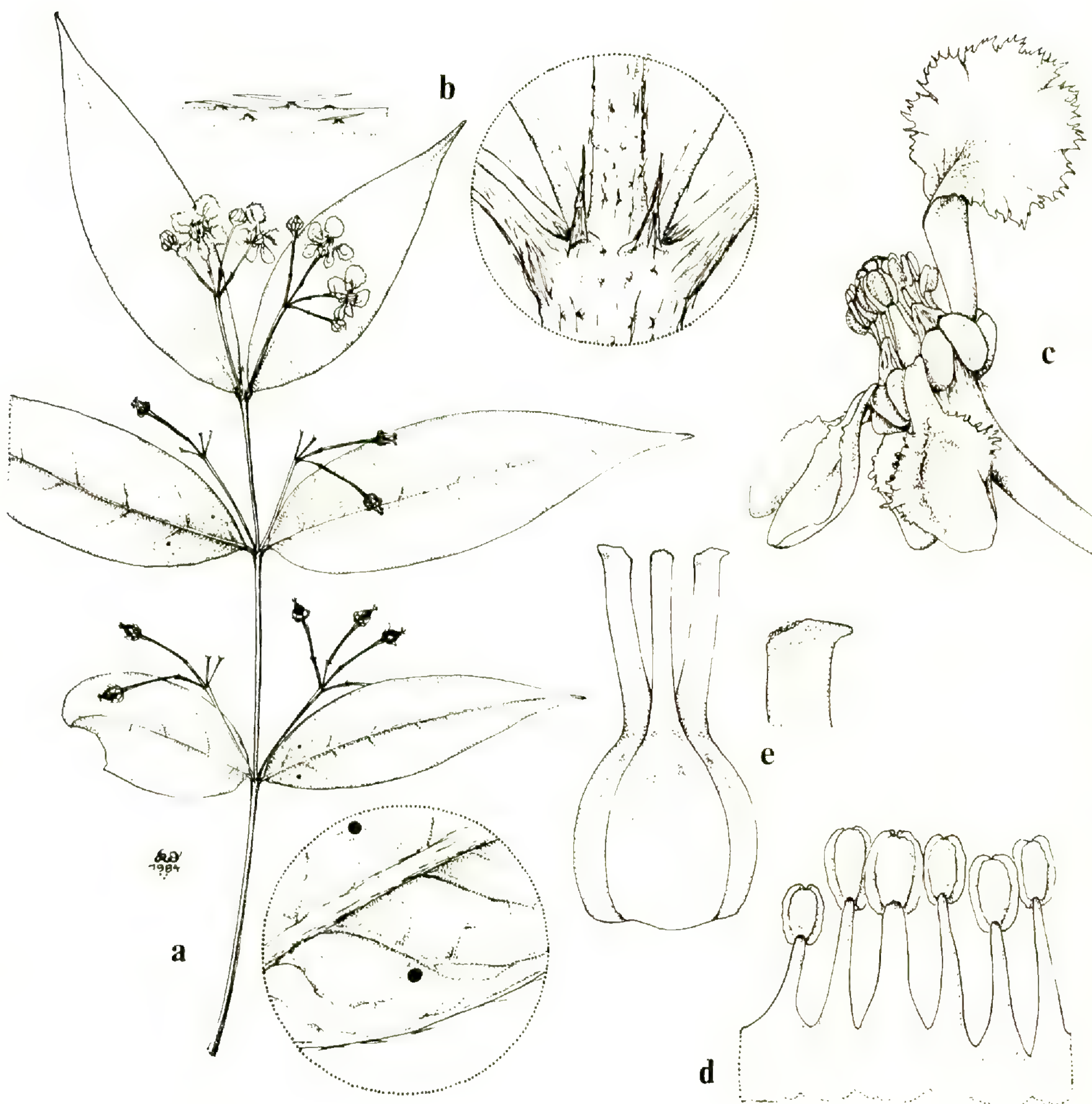


FIG. 17. *Malpighia wilburiorum*. a) habit, $\times 0.75$, with enlargement of abaxial surface of lamina, $\times 10$; b) node, showing stipules, $\times 7.5$, and (to left) stem hairs borne on peglike bases, $\times$ ca 13; c) flower, side view with posterior petal erect, $\times$ ca 5; d) partial androecium, laid out, abaxial view, the stamen at left opposite posterior petal, $\times 10$; e) gynoecium, anterior style in middle, $\times 10$, with apex of 1 style to right, $\times 20$. Drawn by Karin Douthit from the type.

species which has sessile stem hairs, lacks stout yellowish leaf hairs, bears only six glands on the nearly glabrous calyx, and has glabrous petals. It is not known on the Pacific slope of Mexico from west of Oaxaca. The species that is probably most closely related to *M. wilburiorum* is *M. galeottiana* Adr. Juss., which grows in the dry thorn-scrub of Puebla and Oaxaca, where it reaches a stature of 6 m but is usually smaller. The two species are similar in their pegged stems and stout leaf hairs, and in details of the flowers, but in *M. galeottiana* the leaves are much smaller, seldom over 4 cm long, ovate with the apex acute or obtuse, and separated by shorter internodes; also, its umbels are raised on stalks seldom over 5 mm long. *Malpighia galeottiana* and *M. wilburiorum* seem to constitute a species-pair somewhat analogous to *M. novogaliciana* and *M. souzae*, but in this case the species found in Nueva Galicia grows in a more mesic habitat and has larger vegetative parts than the eastern member of the pair.

Mascagnia mesoamericana W. Anderson, sp. nov.

Foliorum majorum lamina 6.5–13 cm longa, 2.5–5 cm lata, apice acuminata, chartacea, petiolo 4–8 mm longo. Bracteae bracteolaeque persistentes vel bracteae demum deciduae, 2.5–5 mm longae, late ovatae vel suborbiculares, multis glandulis marginalibus stipitatis instructae. Sepala adaxialiter glabra vel apice tomentosa, multis glandulis marginalibus stipitatis 0.5–0.9 mm longis instructa. Samara 22–42 mm lata, forma papilionis, nuce hispida pilis 1.5–2.5 mm longis, basifixis vel sub-basifixis, alis lateralibus usque ad nucem divisis.

Woody vine; stems sericeous to glabrate. Lamina of larger leaves 6.5–13 cm long, 2.5–5 cm wide, elliptical or narrowly elliptical, gradually narrowed to a cuneate or rounded base, acuminate at apex, chartaceous, initially sericeous but soon glabrate on both sides, eglandular or bearing several tiny sessile marginal glands on each side in proximal $\frac{1}{2}$, the tertiary nerves hardly or not at all sclariform, the reticulum prominulous below or on both sides; petiole 4–8 mm long, sericeous to glabrate, bearing 0–6 small glands in 2 rows; stipules small, triangular, borne on base of petiole. Flowers borne in tomentose axillary and terminal pseudoracemes or panicles, the ultimate pseudoracemes 3–9 cm long and containing 8–20 flowers; bracts and bracteoles persistent or the bracts deciduous in fruit, 2.5–5 mm long, broadly ovate or suborbicular, abaxially densely appressed-tomentose, adaxially glabrous or tomentose at margin, bearing many long-stalked clavate marginal glands; peduncle 3–5 mm long (–9 mm in fruit), bearing the bracteoles at its apex; pedicel 3–5 mm long. Sepals separating to expose petals well before anthesis, 3–4.5 mm long, 1–1.5 mm wide, triangular, bearing many stalked capitate glands 0.5–0.9 mm long on margin, abaxially appressed-tomentose, adaxially glabrous or tomentose at apex, each of the lateral 4 bearing 2 large abaxial glands 1.5–2 mm long, distally free and often recurved, the anterior sepal without abaxial glands. Petals yellow (?), abaxially densely appressed-tomentose, flat, fimbriate all around margin with fimbriae sometimes glandular-thickened; lateral petals with the claw 1.5–1.8 mm long, the limb elliptical, 4–7.5 mm long, 2.5–4.7 mm wide; posterior petal with the claw 3 mm long, the limb ovate, 5.5 mm long, 4–4.5 mm wide. Filaments very unequal, 4 mm long opposite anterior sepal, 2.2–3 mm long opposite lateral sepals and petals, 1.5 mm long opposite posterior petal, much thickened opposite 2 posterior-lateral petals, glabrous, straight, connate at base; anthers 0.8–1.2 mm long, glabrous. Ovary densely hispid; styles 2.5–3 mm long, bowed at base and then erect, dorsally truncate or apiculate at apex. Samara 22–42 mm wide, butterfly-shaped, hispid on nut, dorsal wing, and proximally on lateral wings with the hairs 1.5–2.5 mm long, basifixed or sub-basifixed, erect, borne at glandular dots, sparsely sericeous distally on wings with the hairs medifixed and appressed; lateral wings 10–20 mm wide, 15–30 mm high, trapezoidal, divided to nut at base and apex, the angle between wings widely obtuse, undulate or coarsely dentate at margin; dorsal wing 4–5 mm wide, wavy (i.e., not lying in 1 plane), $\pm$ entire; intermediate winglets none; ventral areole ovate, 2–2.5 mm high, 1.3–1.8 mm wide.

TYPE: GUATEMALA. Retalhuleu: Mixed forest along road between Retalhuleu and Nueva Linda, 120–220 m, 16 Feb 1941 fr, *Standley 87301* (F, holotype; US, isotype).

PARATYPES: MEXICO. Chiapas: Libertad, Acacoyagua, 700 m, Jan fl, *Matuda 18577* (F).—GUATEMALA. Retalhuleu: Type locality, Feb fr, *Standley 87257* (F).—PANAMA. Darién: 10 km NE of Jaqué, slopes of Río Tabuelitas above Birogueirá, Indian village on Río Jaqué below mouth of Río Pavarandó, to 120 m, Jan fl, *Sytma & D'Arcy 3278* (MICH, MO).

This species is similar to *Mascagnia glandulifera* Cuatr., which has a thicker, broader, more abruptly acuminate leaf blade with notably scalariform veins, a longer petiole, caducous bracts, the sepals tomentose on both sides, and a larger, orbicular samara with the lateral wings continuous at the base. The disjunct distribution of the known collections leads me to expect that *M. mesoamericana* will eventually be found in the Atlantic lowlands of Costa Rica and Nicaragua.

The label of Sytsma & D'Arcy 3278 says of this plant: "Tree, to 4 m tall, flowers whitish tan." I doubt that either statement is correct. The plant is most likely a woody vine, and its petals are probably yellow.

***Mascagnia paludicola* W. Anderson, sp. nov.**

Foliorum majorum lamina 17–21.5 cm longa, 8–12.5 cm lata, chartacea, primo sericea mox glabrata, petiolo 15–20 mm longo, 2 (–6) glandulis instructo. Bracteae bracteolaeque 2–3 mm longae, ovatae, eglandulosae vel aliquot glandulis minutis subsessilibus marginalibus instructae. Sepala multis glandulis marginalibus sessilibus vel brevistipitatis instructa. Samara sparsim sericea pilis medifixis vel glabrata, alis lateralibus 21–24 mm latis, 39–48 mm altis, basi apiceque usque ad nucem divisis.

Woody vine; stems sericeous to glabrate. Lamina of larger leaves 17–21.5 cm long, 8–12.5 cm wide, broadly elliptical, cuneate or rounded at base, acute or abruptly acuminate at apex, chartaceous, initially sericeous but soon nearly glabrate on both sides, bearing several sessile marginal glands on each side in proximal $\frac{1}{2}$, the reticulum prominent on both sides; petiole of larger leaves 15–20 mm long, sericeous to glabrate, bearing 2 (–6) glands in 2 rows; stipules minute, triangular, borne on petiole just above its base. Flowers borne in loosely sericeous axillary and terminal pseudoracemes or panicles, the ultimate pseudoracemes 4–10 cm long and containing 8–24 flowers; bracts and bracteoles soon deciduous, 2–3 mm long, ovate, abaxially loosely sericeous, adaxially glabrous, eglandular or bearing several tiny subsessile marginal glands; peduncle 2–3.5 mm long, bearing the bracteoles at its apex; pedicel 4–5 mm long. Flower parts seen only as remnants in fruit. Sepals 3.5–4.5 mm long, 1–1.5 mm wide, narrowly elliptical, each bearing all around margin a row of small capitate sessile or subsessile glands (the stalks up to 0.2 mm long), densely appressed-tomentose abaxially, sparsely so adaxially, each of the lateral 4 bearing 2 large abaxial glands 2–2.7 mm long, the anterior with 0–1 abaxial gland. Petals apparently densely tomentose on both sides. Anthers ca 1 mm long, glabrous. Styles glabrous, apparently straight, short-hooked dorsally at apex. Samara 50–55 mm wide, suborbicular, sparsely sericeous to glabrate, the hairs medifixed, some borne at glandular dots; lateral wings 21–24 mm wide, 39–48 mm high, divided to nut at base and apex, undulate and denticulate at margin; central dorsal wing 6–8 mm wide, $\pm$ semicircular, coarsely toothed; intermediate winglets none; ventral areole ovate, 2.5–3 mm high, 2–2.5 mm wide.

TYPE: BRAZIL. Amazonas: Rio Purús, Rio Ituxi, Seringal Jurucua, 120 km S of Lábrea, várzea forest, 29 Jun 1971 fr, *Prance et al. 13918* (INPA, holotype; MICH, NY, isotypes).

The name of this species, which means swamp-dweller, is given because it was collected in várzea, a type of Amazonian forest seasonally inundated by white-water rivers. It is closely related to the preceding species, *M. mesoamericana* W. Anderson, and to *M. glandulifera* Cuatrecasas. Both of those species have smaller leaves, larger bracts and bracteoles that bear many stalked marginal glands, and

longer-stalked marginal glands on the sepals. In *M. glandulifera*, which is also a species of western Amazonia, the samara bears mostly basifixed hairs and its lateral wing is continuous at the base.

***Tetrapteryx cordifolia* W. Anderson, sp. nov.**

Frutex 1–3 m altus. Foliorum majorum lamina 2.4–4.3 cm longa, 2.4–4.1 cm lata, late ovata, oblata, vel orbicularis, basi cordata vel rotundata, apice late obtusa vel rotundata et apiculata, coriacea, subtus utrinque 5–11 glandulis marginalibus instructa, reticulo utrinque prominenti; petiolus 1–1.5 mm longus. Flores in pseudoracemo elongato terminali 10–20-floro portati; bracteolae 1–2 mm longae, 0.4–0.8 mm latae, plerumque una abaxialiter 1–2-glandulifera. Sepala omnia biglandulosa. Petala staminaque glabra. Stigma apicale.

Shrub 1–3 m tall, with slender, wiry, sericeous to glabrate branches. Leaves ascending-appressed (?); lamina of larger leaves 2.4–4.3 cm long, 2.4–4.1 cm wide, broadly ovate, oblate, or orbicular, cordate or rounded at base, broadly obtuse or rounded and mostly apiculate at apex, coriaceous, initially sericeous but very soon glabrate on both sides, bearing below a row of 5–11 tiny glands on each side at or just within margin, these mostly in distal $\frac{3}{4}$ of lamina, the lateral veins and reticulum prominent on both sides; petiole 1–1.5 mm long, soon glabrate, eglandular; stipules minute nubbins ca 0.1 mm long, borne on stem at base of petiole, lacking from most nodes. Inflorescence an unbranched elongated terminal pseudoraceme, thinly stramineous-sericeous to glabrate, comprising 10–20 or more flowers that are proximally decussate but distally inserted irregularly; bracts 1.5–2.5 (–3) mm long, 0.4–0.8 mm wide, narrowly triangular or ovate, eglandular or with 1–2 small marginal glandular spots, sparsely sericeous or nearly glabrous; peduncle 4.5–8 mm long; bracteoles 1–2 mm long, 0.4–0.8 mm wide, elliptical or ovate, spreading, sparsely sericeous or nearly glabrous, borne slightly to well below apex of peduncle, opposite or, more commonly, borne at different heights, the more proximal one, or occasionally both, bearing 1 or occasionally 2 large abaxial marginal glands; pedicel 6–8 mm long. Sepals 2 mm long beyond glands, 1.5 mm wide, triangular, obtuse or rounded at apex, appressed in anthesis, abaxially thinly sericeous, ciliate on margin, adaxially glabrous, all 5 biglandular, the glands 2–2.7 mm long, 0.8–1.1 mm wide, narrowly obovate or elliptical, compressed, decurrent. Petals yellow, glabrous; lateral petals with the claw 1 mm long, the limb ca 7 mm long, 5 mm wide, quadrate or obovate, cuneate at base, denticulate or erose at margin; posterior petal hardly different from laterals, the claw slightly longer (1.5 mm), the limb somewhat crumpled. Filaments white distally, red proximally, glabrous, connate just at base, straight, longer (2–2.4 mm) and narrower opposite sepals, shorter (1.5 mm) and wider opposite petals; anthers ca 1 mm long, glabrous, the connective somewhat swollen at apex, especially in anthers opposite petals. Ovary ca 1 mm high, sericeous, 3-carpellate, each carpel bearing 4 primordial lateral wings, 2 on each side, the lower pair larger than the upper pair; styles 3, green, glabrous except just at base, 1.9–2.2 mm long, the anterior slightly longer than the posterior 2, straight, erect, the stigmas apical and without any dorsal angle or extension. Fruit not seen.

TYPE: BRAZIL. Amazonas: Plateau of northern massif of Serra Aracá, 0°51–57'N, 63°21–22'W, south side of North Mountain, 1200 m, plateau savannah, 12 Feb 1984 fl, *Prance et al.* 29005 (INPA, holotype; MICH, NY, isotypes).

PARATYPES: BRAZIL. Amazonas, same locality and probably same population as type, Feb fl, *Amaral* 1550 (MICH), *Prance et al.* 29002 (INPA, NY).

This distinctive species is very similar to *Tetrapteryx cardiophylla* Nied., which differs in having only 1 pair of leaf glands, toward the base of the lamina and set in from the margin; a short, often corymbose pseudoraceme with up to 6 (–8?) strictly decussate flowers and loose white vesture; much larger and more leaflike bracteoles (3–4 mm $\times$ 1.4–2.5 mm in the specimens I have seen); 8 calyx glands, the anterior sepal being eglandular; and internal stigmas. *Tetrapteryx cardiophylla* is a rare species endemic to the Serra do Sincorá in Bahia, Brazil, far from the Serra Aracá. A similar case is that of *Verrucularia piresii* W. Anderson, endemic to the Serra Aracá, and *V. glaucophylla* Adr. Juss., another species of the Serra do Sincorá in Bahia (Anderson 1981, pp 45–48). The upland flora of the Serra Aracá apparently contains relictual elements of a savannah flora that must have formerly been much more widespread, probably during the dry periods of the Pleistocene when the wet forest had withdrawn to refugia.

ACKNOWLEDGMENTS

Much of the research presented here was supported by a grant from the National Science Foundation to The University of Michigan (DEB-8103522). James White of the Hunt Institute for Botanical Documentation sent me a set of color transparencies of the Malpighiaceae in the Torner Collection of Sessé and Mociño Biological Illustrations, and the following botanists kindly assisted me when I was doing fieldwork and visiting foreign herbaria: C. Cristóbal, G. Hatschbach, A. Krapovickas, S. Koch, E. Lott, A. Lourteig, P. Occhioni, L. M. V. de Puga, J. Rzedowski, A. Schinini, and M. Sousa. I am also grateful to the curators of the herbaria represented by the following acronyms for gifts and loans of Malpighiaceae: CEPEC, CHAPA, DUKE, ENCB, F, GB, GH, IAN, INPA, K, MBM, MEXU, MG, MO, NY, P, QCA, RB, S, SEL, UB, UC, US. The lovely drawings were made by Karin Douthit.

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REVISIONS OF HYBOCHILUS AND GONIOCHILUS (ORCHIDACEAE)

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In the course of preparing a monograph of the oncioid orchid genus *Leochilus* Knowles & Westc. (Chase 1986c), the two species of the Central American genus *Hybochilus* Schltr. were collected and examined in order to determine their relationships to the species of *Leochilus*. Both these species have been rarely collected and are widely misunderstood. They have small, fleshy, complex flowers (especially *H. inconspicuus*) that are difficult to interpret once they are pressed and dried. This study thus benefits from the availability of live material. *Hybochilus inconspicuus* (Kränzlin) Schltr., the type species of *Hybochilus*, was found to be only distantly related to *Leochilus*, whereas *H. leochilinus* (Reichb. f.) Mansf. was determined to be a near relative. A number of significant features distinguish these two species, and these differences indicate that *H. leochilinus* cannot be maintained in *Hybochilus*. Additionally, it does not conform to the features of any other oncioid genus, and a new monotypic genus, *Goniochilus*, is proposed for this species.

MATERIALS AND METHODS

Herbarium specimens were borrowed from the following herbaria: F, G, K, MO, NY, SEL, US, and W. I also visited AMES and CR. Live material of *Hybochilus inconspicuus* from one locality and *Goniochilus leochilinus* from three localities in Costa Rica was also examined. The live plants were mounted on slabs of sassafras and grown in greenhouses at the Natural Sciences Building on the campus of the University of Michigan.

The illustrations in this paper were prepared from live material drawn with the aid of a drawing tube mounted on a dissecting stereomicroscope. Flowers and fruits of my numbered collections (MWC) were preserved in a modified FAA (53% ethanol, 37% water, 5% formaldehyde, and 5% glycerol). These will later be deposited in a major herbarium. When my collections represented new localities, specimens were pressed and deposited at CR and MICH. Pollinia were removed from live flowers, photographed on a Wild dissecting stereomicroscope, and then stored in gelatin medicine capsules. Scanning electron micrographs of the seeds were made on an Hitachi S570. All specimens were simply air dried before gold coating.

ECOLOGY AND DISTRIBUTION

Both *Hybochilus inconspicuus* and *Goniochilus leochilinus* are twig epiphytes and exhibit the features and traits associated with this habitat specialization (Chase 1986a, c). Like *Leochilus*, these two species move onto cultivated plants

and are more common than the paucity of collections would indicate. They have often been collected on *Citrus*, *Coffea*, and *Psidium guajava*. I did not observe either of them in primary forest, but I suspect, also like *Leochilus*, that they occur on small branches and twigs in the upper parts of the forest canopy. The localities I observed and the data from herbarium sheets indicate that they inhabit sites that never get as dry as those of some species of *Leochilus*. Cloud and moderate elevation rain forests (500–1500 m) appear to be their only habitat type, whereas *L. scriptus* (Scheidweiler) Reichb. f. also occurs on the seasonally dry Pacific side of Central America.

On cultivated plants, they may occur in relatively dense populations. I observed as many as 50 plants of *G. leochilinus* growing on single guava and orange trees in pastures (500 m) near Cariblanco (Alajuela Province), Costa Rica, in the Atlantic watershed. Similar numbers were also observed on guava in cloud forest (1500 m) near San Ramón (Alajuela Province), Costa Rica.

Oncidioid twig epiphytes are restricted to the outer branches of their hosts, and the rodriguezioid twig species (clade B; Chase 1986a) have a number of features associated with this habitat, including psygmoid habit (fanshaped with laterally flattened leaves and no pseudobulbs) in the seedling stage and elongate seeds with hooked ends (Chase 1986c). Lower chromosome numbers ($2n = 36-48$) also are associated with oncidoid twig epiphytism, but I made no counts for either of these species.

Many species that inhabit the trunks and other larger axes of their host take from five to seven years to reach maturity, but most of the oncidoid twig epiphytes do so in a single season (Chase 1986c). I did not observe these two species in a way that will permit me to state conclusively that they also have such speeded up life cycles, but they both exhibit the features observed for *L. labiatus* (Sw.) Kuntze and *L. scriptus* (Chase 1986c), which do have nearly an annual type of life history. These features are: blooming at small size and producing only a fraction of the number of flowers a large specimen produces; flowering on the first growth produced (they produce an annual sympodium; their age is the number of such growths present); ripening capsules in two to three months (*H. inconspicuus* only) instead of the typical ten to twelve; occurring in populations consisting of largely first-bloom plants; and only rarely living to be three or more years old.

I did not observe pollinators for either species, but their floral morphology and dull coloration suggests lower hymenopterans, much as was observed for *Leochilus* (Chase 1986b). *Leochilus* has a relatively open nectary that made access by polistine and polybiine wasps and halictid bees possible. They merely had to climb into the nectar cavity. Both *H. inconspicuus* and *G. leochilinus* have nectar cavities that are enclosed in such a way that I suspect access is only by the insect's tongue. In fact, they have a central groove that would guide the tongue into the nectary. The pollinarium may be attached to the mouth parts of the pollen vector of *H. inconspicuus* because of the relationship of the lip to the column and because the viscidium is long and narrow (the latter a feature that often occurs when the viscidium is attached to the tongue). The column-lip arrangement of *G. leochilinus* may result in pollinarium attachment on the thorax because, to gain access to the nectary, the insect would have to work its way a considerable distance into the channel in front of the cavity itself and probably contact the viscidium only when it backed out.

I observed only a small amount of nectar production in *G. leochilinus* and none in *H. inconspicuus*. Most of the species of *Leochilus*, however, do not produce nectar under greenhouse conditions, but those examined under field

conditions (seven of the nine species) all do so. My observations under cultivation may thus not be representative of what occurs in nature.

Both *Hybochilus* and *Goniochilus* are of restricted distribution; *H. inconspicuus* has been collected in the mountains around the Central Valley of Costa Rica and Chiriquí Province in western Panama, while *G. leochilinus* occurs in the Atlantic watershed and the Cordillera Central of Costa Rica, Nicaragua, and western Panama.

This distribution is typical of most genera of rodriguezioid orchids, which are all twig epiphytes. The group is more numerous and diverse away from the center of familial diversity in the Andes of South America. Of the larger grouping of related genera (discussed below), only *Konantzia* Dodson & N. H. Williams is Andean. *Capanemia* Barb. Rodr. is from southern Brazil, *Polyotidium* Garay and *Quekettia* Lindley are from northeastern South America, *Papperitzia* Reichb. f. is North American, and *Ionopsis* Kunth and *Trizeuxis* Lindley are found at lower elevations throughout the Neotropics, whereas *Leochilus* has the same general distribution as the last two genera but is most diverse in Central and North America.

Both *H. inconspicuus* and *G. leochilinus* are often microsympatric with *L. labiatus*. I observed the last growing with *G. leochilinus* on guava and orange trees near Cariblanco (Alajuela Province), Costa Rica, and a number of mixed collections indicate microsympatry for *L. labiatus* and *H. inconspicuus*. All three species occur near San Ramón (Alajuela Province), Costa Rica, but have not been collected at the same microsites. The flowering seasons of all three species overlap somewhat, but I have seen no putative instances of hybridization (I did not perform crossing experiments to determine if hybridization is possible).

COMPARATIVE MORPHOLOGY

Hybochilus and *Goniochilus* have a generalized oncidoid habit: ancipitous (two-edged, dorso-ventrally compressed), more or less globose pseudobulbs; conduplicate leaves; and laterally produced inflorescences. They may have one or two apical leaves and from one to five basal sheathing leaves that grade into a series of sheathing, basal bracts. They are small, caespitose herbs and have no unique vegetative features, although, once familiar with them, one can usually identify them in sterile or fruiting condition.

The seedlings of both species are psygmoid, i.e., fanshaped with laterally flattened leaves and no pseudobulbs. This is the typical habit for seedlings of the rodriguezioid group, and they are often mistaken for small plants of the distantly related genus *Ornithocephalus* Hook., which has this same general habit. As the first season of growth is completed, flowering occurs concurrently with production of pseudobulbs and conduplicate leaves. Both *H. inconspicuus* and *G. leochilinus* make a complete transition to adult morphology, unlike *Macroclinium* Barb. Rodr. ex Pfitzer, *Plectrophora* Focke, and *Trizeuxis*, which retain, to varying degrees, the seedling habit into the adult stage.

The inflorescence of *H. inconspicuus* is an erect to pendent primary panicle, whereas that of *G. leochilinus* is always pendent and usually a raceme that may secondarily become paniculate. I use the term "primary" to indicate that the side branches are produced simultaneously with the main axis. In *Goniochilus*, *Leochilus*, and a number of other genera, the inflorescence is initially nearly always a raceme that will, if no or only a few fruits are set, initiate a series of lateral racemes. This is a primary raceme that may become secondarily paniculate. Robust specimens of this latter type may produce a weakly paniculate primary inflorescence.

The flowers of *H. inconspicuus* may be held with the lip lowermost, a position that is obtained by the twisting of the ovary if the inflorescence is erect. On pendent inflorescences, the flowers usually face downward, and the lip is nearest the axis, which is its position in bud. The flowers of *G. leochilinus* always face downward on a limp, pendent inflorescence. This flower position is rare in the oncioid orchids, although it is standard in other neotropical genera, such as *Stanhopea* Hook. *Leochilus oncioides* Knowles & Westc. also has a pendent inflorescence, but, in contrast, the flowers typically face outward with the lip lowermost.

The sepals and petals of both *H. inconspicuus* and *G. leochilinus* are abaxially carinate, but this is not a taxonomically useful feature since it occurs in most oncioid species. The lateral sepals are usually connate up to $\frac{3}{4}$ their length but may be free in the latter. This trait is also variably expressed within many other genera, such as *Leochilus*. In *G. leochilinus*, the bases of the lateral sepals are shortly adnate to the lip base.

The lip of *H. inconspicuus* is trilobate, with the lateral lobes basal and erect. The lip base forms a glabrous nectar cavity with an obscuring front wall adjacent to the bilobed lip callus. This type of lip morphology is similar to that of *Polyotidium* and is entirely different from that found in *Goniochilus* and *Leochilus*. In both these genera, the cavity is furnished with its own front wall (notched in some species of *Leochilus* and in *Goniochilus*), and the lip callus is a separate structure located somewhat forward of the nectary in *Leochilus* and much forward in *Goniochilus*. In *Goniochilus*, the notched front wall is covered with long hairs that obscure its presence.

The lip of *G. leochilinus* is also trilobate, but the lateral lobes are produced near the midpoint of the lip rather than at the base, as in *H. inconspicuus*, and do not form the nectary side walls. Additionally, the apical half of the lip is bent at a 90° angle relative to the basal portion. In both species, the midlobe is retuse.

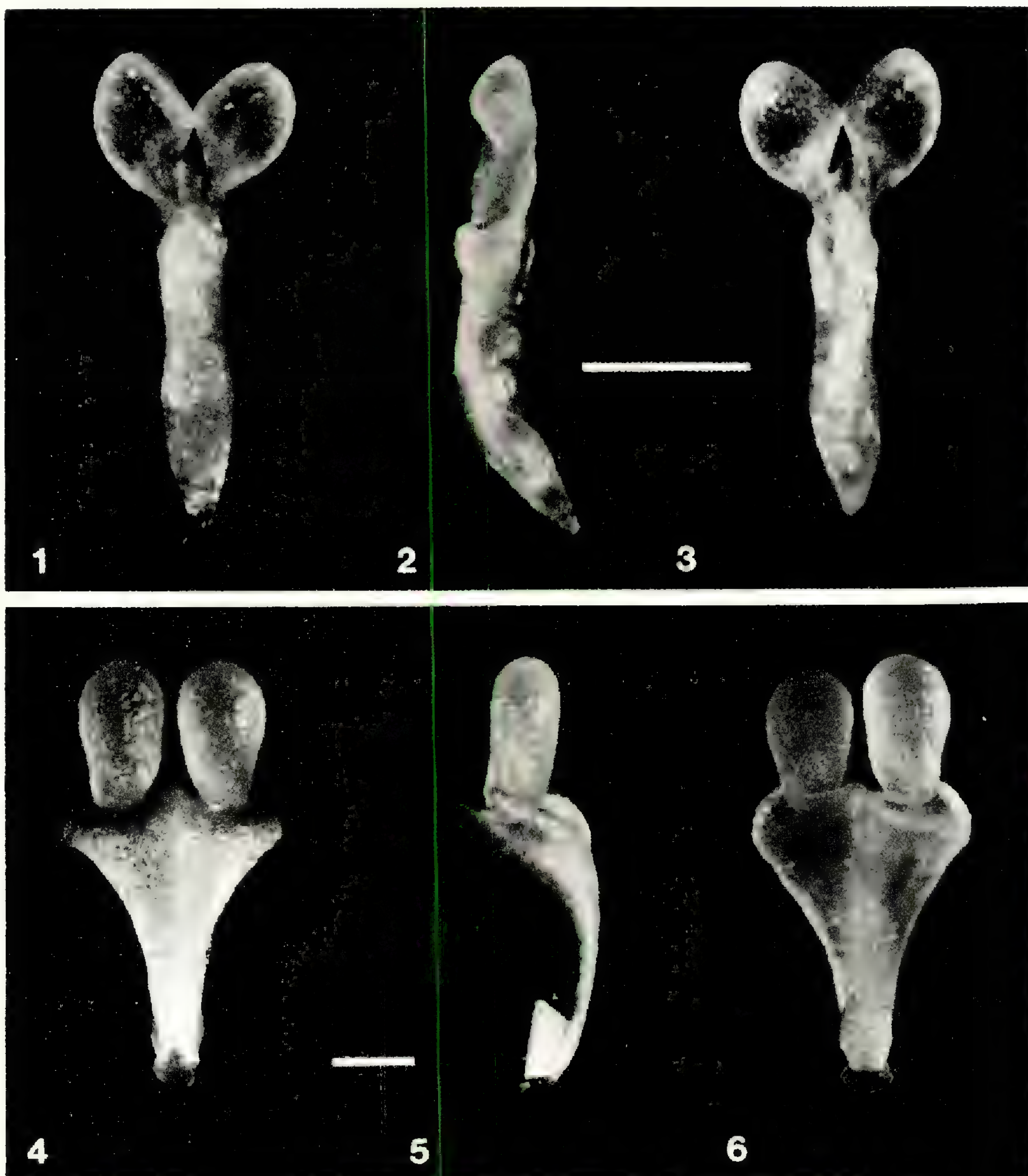
As is the case with most orchid genera, the column is of great systematic importance. These features in combination with lip morphology distinguish these two genera from their close relatives. Neither genus has a tabula infrastigmatica, as in *Oncidium* and its relatives, or a column foot, as in *Ionopsis*. The complex stigma of *H. inconspicuus* is located immediately below an elongate, bifurcated rostellum, and its opening is oriented perpendicularly to the column axis. The inner lobes of the bilobed stigmatic arms form a v-shaped groove. The short, bilobed, extrorse stigmatic arms are situated on the sides of the stigma. *Polyotidium* and some species of *Rodriguezia* have both stigmatic and column arms, but in *H. inconspicuus* the two parts appear to have the same origin and are in the same plane, so I consider them to be merely bilobed stigmatic arms rather than two sets of distinct arms.

In *G. leochilinus*, a more or less circular stigmatic cavity is located a short distance from the column apex, and the two, extrorse stigmatic arms are much longer and unlobed. In contrast, the stigma in *Leochilus* occurs nearly at the midpoint of the column, and the arms are perpendicular to the column axis.

The anther cap in *H. inconspicuus* is relatively long and hinged and is situated terminally on the apex of a short (only $\frac{1}{5}$ the length of the lip) column. In *G. leochilinus*, the anther cap is also elongate but unhinged. As in *Rodriguezia*, the anther of *G. leochilinus* is located dorsally on an elongate ($\frac{1}{2}$ the length of the lip) column and has a pronounced clinandrial protusion located below the stipe. This anther is not as dorsal as in *Notylia*, but it is much more so than in

Hybochilus and *Leochilus*. The substipular protrusion is also lacking in the latter two genera.

The pollinaria of *H. inconspicuus* and *G. leochilinus* are different from each other and distinctive among the rodriguezioid genera. The former has dorsoventrally flattened and twisted pollinia that are oriented in a plane corresponding with its narrow stigmatic opening. The great majority of oncidioid species have globose pollinia and more or less circular stigmatic cavities. The major exception is *Notylia* and its close relatives, in which laterally flattened pollinia fit into a longitudinal stigmatic slit. The stipe of *H. inconspicuus* is slightly enlarged in the middle. Its head is somewhat tubularized, and the pollinia are inserted into two lateral depressions on its apex. This species also has a two-parted viscidium, but the proximal portion is not as well developed as in *Goniochilus* and *Leochilus*. The viscidium of *H. inconspicuus* is quite unusual among the rodriguezioid orchids in that it is nearly as long ($\frac{2}{3}$) as the stipe and has a pronounced ventral ridge that extends below the rostellum (Figs. 1–3).



FIGS. 1–6. Views of the pollinaria of *Hybochilus* and *Goniochilus*. 1–3. *Hybochilus inconspicuus*, Costa Rica (MWC84308). 1. Adaxial view. 2. Side view. 3. Abaxial view. 4–6. *Goniochilus leochilinus*, Costa Rica (MWC84210). 4. Adaxial view. 5. Side view. 6. Abaxial view. (Scale bar = 0.5 mm.)

The pollinarium of *G. leochilinus* has oblong pollinia inserted into two depressions on a greatly enlarged stipe head. The two parted viscidium of this species is oval and much shorter ($\frac{2}{3}$) than the stipe (Figs. 4–6).

The capsules of both species are typical of most rodriguezioid genera; i.e., they are deltoid, beaked, and dehisce by the three valves splitting along their edges and bending outward. The mature fruits of *H. inconspicuus* are short (1.0–1.5 cm) and only slightly beaked (0.2–0.3 cm), whereas those of *G. leochilinus* are much longer (3.5–4.0 cm) and more prominently beaked (0.8–1.0 cm).

The seeds of both species are typical of the rodriguezioid group. They are elongate and have prominent hooks on their ends, particularly the micropylar end (Figs. 7–10). The *Oncidium*-derived twig epiphytes, the “variegata oncidiums,” have a similar elongate shape, but their testa extensions are knobbed rather than hooked (Figs. 11, 12). This difference supports the contention (Chase 1986a) that these two groups have an independent origin.

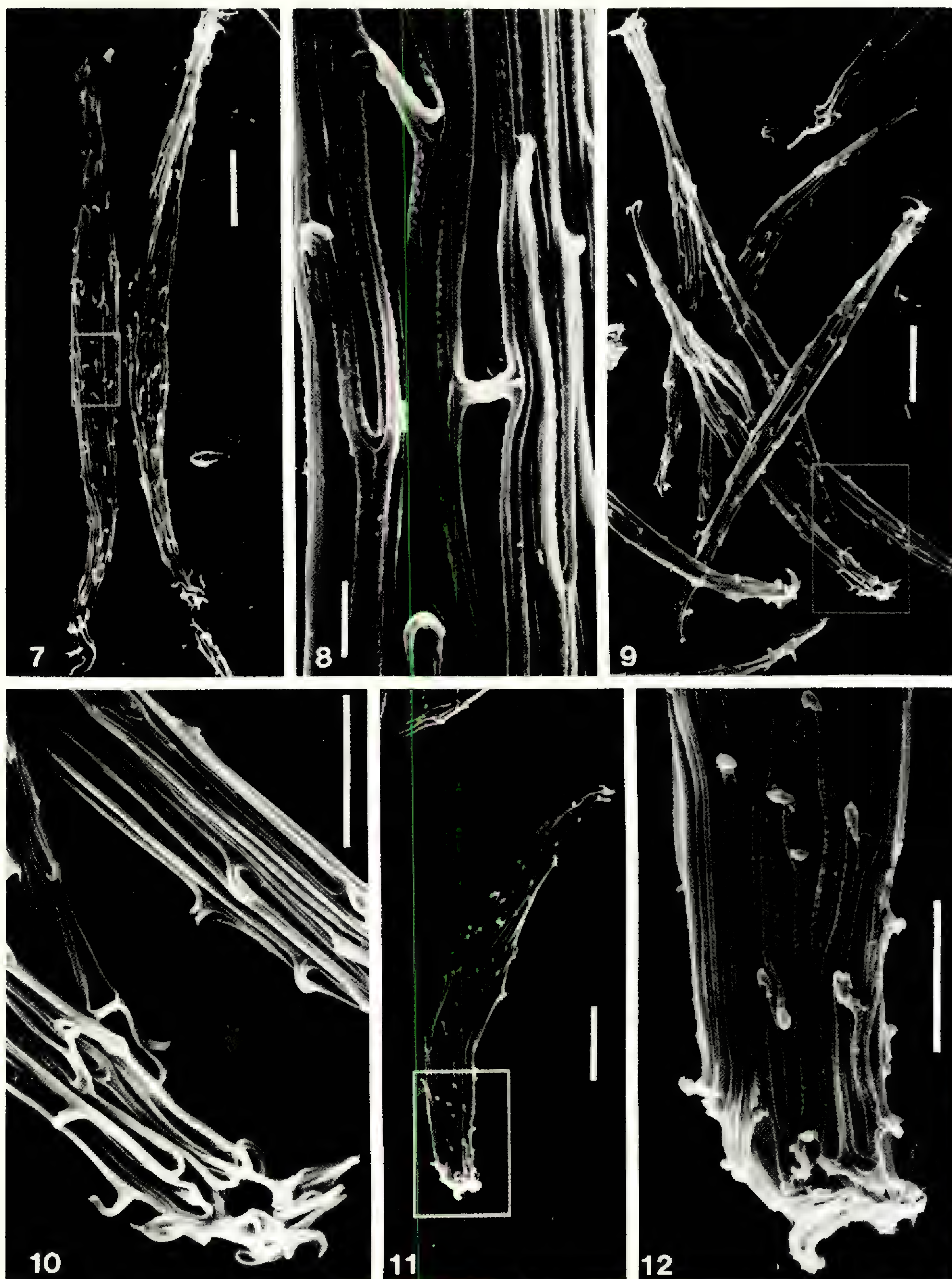
Not all small oncidoid species that occasionally occur on twigs are twig epiphytes. *Rhyncostele pygmaea* (Lindley) Reichb. f., a species as diminutive as *H. inconspicuus* and *G. leochilinus*, may grow, under certain environmental conditions, on smaller axes of its hosts, but it then occurs on limbs of all sizes. This species belongs to the trunk-limb genera related to *Odontoglossum* Kunth and *Oncidium* Sw. (clade A; Chase 1986a), and it has the seeds typical of this group. They are much wider for their length than those of the twig epiphytes and lack the prominent testa extensions (Figs. 13, 14).

Summary. The taxonomically significant features of *Hybochilus*, *Goniochilus*, and the other rodriguezioid genera I consider their closest relatives are presented in table 1. The important features of *H. inconspicuus* are: a glabrous lip nectary that is enclosed in front by a bilobed callus; a lack of lateral sepal-lip adnation; a short column with short bilobed stigmatic arms; a narrow stigmatic opening; a terminal anther; and a pollinarium with dorsoventrally flattened pollina, an indented stipe head, and an elongate, weakly biparted viscidium. *Goniochilus leochilinus* is distinguished from its close relatives by: a shallow nectary with a grooved, pubescent entry channel; a lip callus situated much in front of the nectar cavity; a bent lip; a degree of lateral sepal-lip adnation; an elongate column with extrorse, stigmatic arms; a dorsally situated anther with a substipular protuberance; and a pollinarium with a greatly enlarged, indented stipe head and a small, strongly biparted viscidium.

GENERIC RELATIONSHIPS

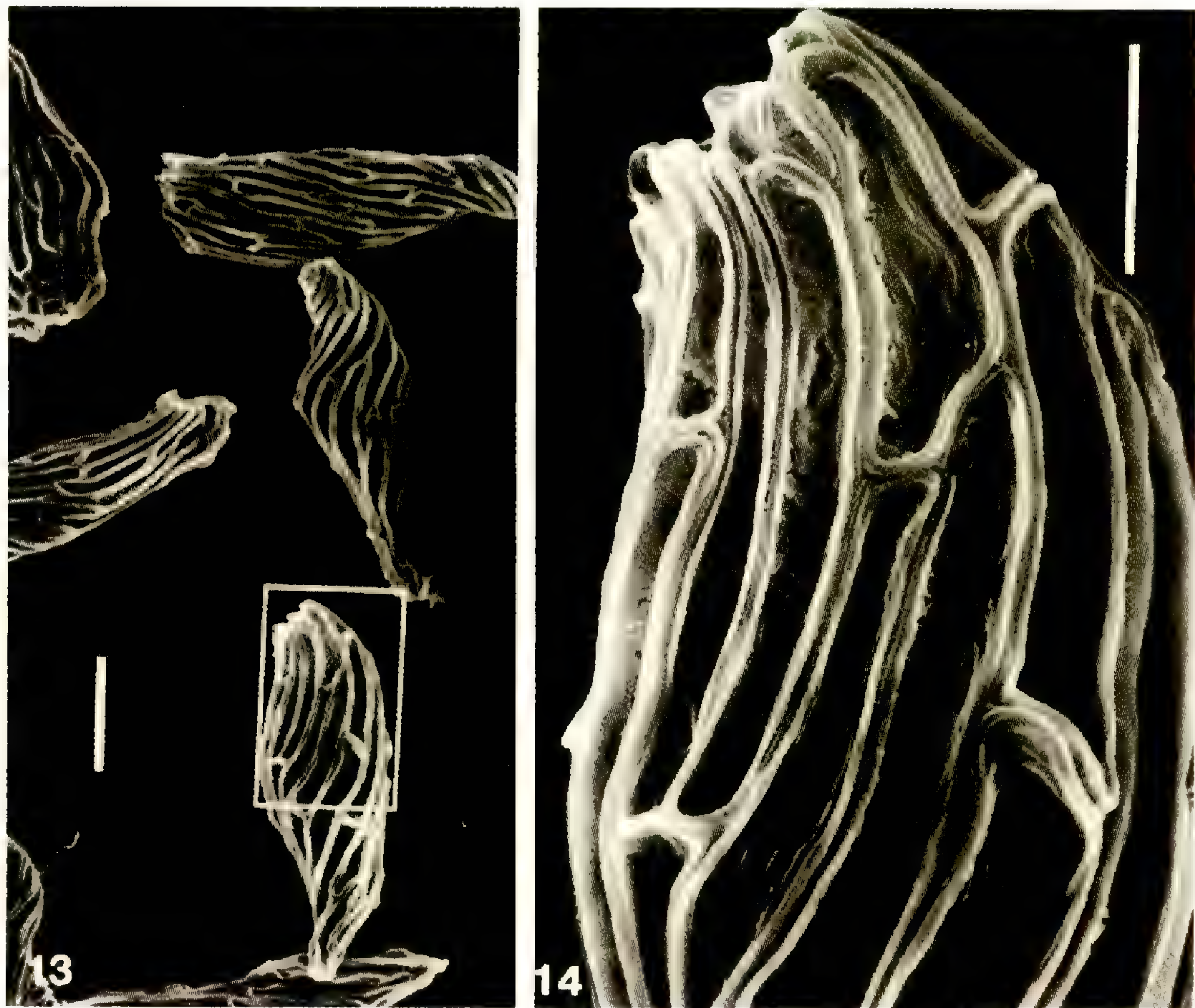
Hybochilus and *Goniochilus* clearly belong to the rodriguezioid group of the oncidoid orchids. This is a heterogeneous group that has a dimorphic life history (psygmoid seedlings and conduplicate-leaved, pseudobulb-bearing adults) and flowers that lack the complex calli and tabula infrastigmatica of *Oncidium* and its relatives. Within the rodriguezioid group, at least three evolutionary subgroupings occur, and *Hybochilus* and *Goniochilus* belong to the one (table 2) that does not have the nectar horns of *Rodriguezia*, *Comparettia* Peoppig & Endl., and their relatives or a stigmatic slit that parallels the column, as is found in *Macradenia* R. Br., *Notylia*, and their relatives.

Many of the rodriguezioid genera are monotypic and may be considered true “oddities.” *Erycina* Lindley, *Papperitzia*, *Polyotidium*, *Saundersia* Reichb. f., and *Trizeuxis* are difficult to ally closely to any other single genus. Other genera, such



FIGS. 7–12. Seed morphology of twig epiphytes. 7, 8. *Hybochilus inconspicuus*, Costa Rica (Alfaro s.n.; US). 7. Whole seeds. 8. Testa cell morphology. 9, 10. *Goniochilus leochilinus*, Costa Rica (MWC84371). 9. Whole seeds. 10. Hooks on micropylar end. 11, 12. *Oncidium urophyllum* Lindley, Dominica (Wilbur et al. 7668; MICH). 11. Whole seed. 12. Testa extensions on micropylar end. (Scale bar = 0.1 mm in all except 8; in 8, scale bar = 0.01 mm.)

as *Capanemia* and *Quekettia*, are heterogeneous “catch-alls,” and contain species, such as *C. superflua* (Reichb. f.) Garay and *Q. vermueleniana* Determann that appear to represent additional new genera with different affinities from those now considered congeneric.



FIGS. 13, 14. Seed morphology of a trunk-limb species, *Rhyncostele pygmaea*, Mexico (MWC82125; MICH). 13. Whole seeds. 14. Testa cell morphology. (Scale bar = 0.1 mm.)

I consider *Hybochilus* to be allied to *Capanemia*, *Konantzia*, *Polyotidium*, *Quekettia*, and *Trizeuxis*. Its nectary type also occurs in *Polyotidium*, and its pollinarium form is similar to those of *Polyotidium* and *Trizeuxis*, but the flattened, twisted pollinia are unique.

Goniochilus is, as stated earlier, most closely related to *Leochilus*. They both have shallow nectaries that are distinct from the lip callus. The pollinaria of these two genera are similar to each other and to that of *Papperitzia*, although the last has a much more complex floral morphology. *Goniochilus leochilinus* could be considered merely a pendently flowered species of *Leochilus*, but none of its important features occur in any species of *Leochilus*. More importantly, their shared structures are typical of many rodriguezioid genera.

Even though *Hybochilus* and *Goniochilus* have distinctly different floral morphologies from any other rodriguezioid genus, I am loath to create two more monotypic genera. I cannot envision how these fit into any evolutionary pattern except as completely isolated end points that have as their ancestor something similar to *Rodriguezia*. The differences between any of these genera and *Rodriguezia* are, however, numerous and drastic. The alternative to establishing *Goniochilus* is to consider all these species as members of an extremely heterogeneous supergenus (one more diverse than any other orchid genus with which I am familiar).

In contrast to the clearly delineated rodriguezioid group are the oncioid trunk-limb genera (clade A; Chase 1986a). Among these, one has to search diligently to find generic distinctions that do not have intermediates or species that express mixtures of the generic characteristics. Even the closest relatives of

Table 1. Comparison of the genera most closely related to *Hybochilus* and *Goniochilus* (tentatively arranged into four informal alliances).

	anther position	column length	stigmatic arms	lip-lateral sepal adnation	nectar cavity	stigmatic opening
<i>Goniochilus</i>	dorsal	long	extrorse	+	lip base	circular
<i>Leochilus</i>	terminal	long	perpendicular	+	lip base	circular
<i>Papperitzia</i>	dorsal	short	extrorse	+	lip base	elongate scooped
<i>Capanemia</i>	terminal	short	extrorse	—	—	circular
<i>C. superflua</i> group	dorsal	short	extrorse	—	lip base	circular
<i>Hybochilus</i>	terminal	short	bilobed, extrorse	—	lip base*	narrow
<i>Konantzia</i>	terminal	long	none	—	—	circular
<i>Polyotidium</i>	dorsal	long	extrorse	—	lip base*	elongate scooped
<i>Quekettia</i>	terminal	long	introrse, extrorse	—	—	circular
<i>Trizeuxis</i>	terminal	long	none	—	—	v-shaped
<i>Ionopsis</i>	terminal	long	none	—†	lateral sepals	circular
<i>Rodriguezia</i>	dorsal	long	extrorse	—	—	circular
(<i>maculata</i> group)						
<i>Q. vermueleniana</i>	dorsal	long	extrorse	+	lip base	v-shaped

*lip callus forms part of nectary front wall.

†sepals adnate to column foot.

Hybochilus and *Goniochilus* are easy to distinguish, but this cannot be said of *Miltonia* Lindley, *Odontoglossum*, and *Oncidium*.

Of the 18 genera I consider members of the group to which *Hybochilus* and *Goniochilus* belong, 44% (8) are monotypic and another 28% (5) comprise only two species (table 2). I suspect that, once revisionary work is undertaken, the number of monotypic genera will increase substantially because superficially similar species have been lumped in a number of cases.

I do not believe that the high number of small genera is a result of the orchid taxonomist's "splitting" nature. Instead, I suspect this plethora of "oddballs" may be a correlative of twig epiphytism. This extreme and depauperate habitat (Chase 1986a) requires a high degree of specialization, and many, highly specialized groups are low in number. The rodriguezioid twig epiphytes have approximately 190 species, while their relatives that inhabit the trunks and other larger axes have 800 (Chase 1986a). In spite of the disparity in numbers, the number of monotypic genera in each group is nearly the same (17 and 16, respectively).

TAXONOMIC HISTORY

At various times, three species have been placed in *Hybochilus*. The first of these to be described was *Goniochilus leochilinus*. Reichenbach fil. published a relatively nonspecific description of it in 1871 and placed it in *Rodriguezia*. In particular, he mentioned that it was similar to the nectaryless members of that genus, specifically "*R. maculata*," which I assume to be *R. maculata* (Lindley) Reichb. f., rather than *R. maculata* Lindley (= *Leochilus oncidioides*). Reichen-

Table 2. Rodriguezioid genera in the same subgrouping as *Hybochilus* and *Goniochilus*.

	number of species
<i>Antillanorchis</i> Garay	1
<i>Capanemia</i> Barb. Rodr.	15
* <i>Erycina</i> Lindley	1
<i>Hybochilus</i> Schltr.	1
<i>Ionopsis</i> Kunth	5
<i>Goniochilus</i> M. W. Chase	1
<i>Konantzia</i> Dodson & N. H. Williams	1
<i>Leochilus</i> Knowles & Westc.	9
<i>Papperitzia</i> Reichb. f.	1
<i>Plectrophora</i> Focke	4
<i>Polyotidium</i> Garay	1
<i>Quekettia</i> Lindley	6
<i>Rodriguezia maculata</i> (Lindley) Reichb. f. group	9
<i>Rodrigueziopsis</i> Schltr.	2
<i>Sanderella</i> Kuntze	1
<i>Saundersia</i> Reichb. f.	2
<i>Trizeuxis</i> Lindley	1
<i>Warmingia</i> Reichb. f.	2

*I consider *Erycina diaphana* Reichb. f. a synonym of *Oncidium hyalinobulbon* Llave & Lex. and a member of *Oncidium* Sw. allied to *O. cheiroporum* Reichb. f. The removal of this species leaves *Erycina* with only the type species, *E. echinata* Lindley.

bach failed to note a number of important features of this species, such as the presence of a nectary and the dorsally situated anther. The identity of this taxon was not ascertainable from the description, and the species was to remain poorly known to orchidologists until new collections were sent from Costa Rica in the 1920's.

In 1895, Kränzlin described *H. inconspicuus*, also in *Rodriguezia*. Probably for much the same reason as Reichenbach, Kränzlin allied his new species to those of *Rodriguezia* that lack a nectar spur. The latter also have a trilobed lip, but they lack a nectary altogether, and *H. inconspicuus* has a well-developed one formed by the lip base.

That neither of these species had real similarity to *Rodriguezia* did not escape Schlechter, and he stated so when he established *Hybochilus* (1920) as a monotypic genus based on *R. inconspicua* Kränzlin. He allied his new genus with *Trizeuxis*. At that time, Schlechter had not seen material of *Rodriguezia leochilina* Reichb. f., but he did have a sketch sent by Zahlbruckner and Keissler from the Reichenbach herbarium. This drawing did not furnish him with the necessary information, and he left matters as they were, mentioning that *R. leochilina* might represent a second species of *Hybochilus*.

When Schlechter did receive material of *R. leochilina* in 1923, he transferred it, not into *Hybochilus*, but rather into *Mesospinidium* Reichb. f. He apparently saw no reason to place it in *Hybochilus*, but his comments about the transfer indicate confusion over the concept of *Mesospinidium*, which has had a history of being misunderstood. It has often been a "catchall" for species that did not fit well anywhere else. After Schlechter's death, Mansfeld (1938) made the combination in *Hybochilus*, and since it obviously did not belong in *Mesospinidium*, the transfer has been accepted by most later authors.

Before the transfer of *R. leochilina*, Mansfeld (1934) had described a third species and placed it in *Hybochilus*. This entity, *H. huebneri*, was a great deal more similar to *H. inconspicuus* than is *G. leochilinus*, but it too is not closely related. Mansfeld was quite aware of the great number of differences between his new species and *H. inconspicuus*, but he chose not to create for it a new genus. Garay (1958) segregated *H. huebneri* into the monotypic genus *Polyotidium*. Now, with the splitting off of *H. leochilinus*, all three species that have been described as members of *Hybochilus* are placed in monotypic genera.

TAXONOMY

KEY TO FLOWERING AND FRUITING SPECIMENS OF HYBOCHILUS AND GONIOCHILUS

Inflorescence a compound panicle, erect to pendent; flowers 0.3–0.35 cm long; lip with a glabrous, basal nectar cavity with the front wall flush with the callus; stigma located immediately below the forked rostellum and bordered by two, short, bilobed stigmatic arms; anther terminal; pollinia dorsoventrally flattened; capsules 1.0–1.5 cm long with a beak 0.2–0.3 cm long.

Hybochilus inconspicuus.

Inflorescence a weak, pendent raceme (rarely a simple panicle); flowers 1.0–1.8 cm long; lip with a basal nectar cavity with a pilose, notched front wall and a lip callus situated much in front of the nectary; stigma more or less a circular cavity located near the column apex, with two, long, unlobed stigmatic arms; anther dorsal; pollinia globose; capsule 3.5–4.0 cm long with a beak 0.8–1.0 cm long.

Goniochilus leochilinus.

Hybochilus Schltr., Repert. Spec. Nov. Regni Veg. 16: 429. 1920.—TYPE: *Hybochilus inconspicuus* (Kränzlin) Schltr.

Small to medium-sized, short-lived, perennial, caespitose herbs epiphytic on small branches and twigs, with the pseudobulbs clustered on short, creeping rhizomes. Pseudobulbs ovoid to suborbicular, ancipitous, unifoliate or bifoliate, often both conditions present in the same population or even in the same individual, lower portions concealed by 2 or 3 sheathing leaves, uppermost larger, eventually deciduous. Leaves elliptic-lanceolate, coriaceous, glabrous, conduplicate, with an unequally bilobed apex, margins entire, eventually deciduous. Inflorescences produced laterally from the base of a pseudobulb, subtended by a sheathing leaf, moderate to long, primarily a complex panicle, erect to pendent, stiff, many-flowered. Pedicellate ovaries twisted or not, glabrous. Flowers small to minute, weakly colored, inconspicuous, resupinate to pendent. Dorsal sepal free, laterals united up to $\frac{3}{4}$ their length, all sepals subequal, narrowly ovate, dorsally carinate, shortly acuminate, with entire margins. Petals free, similar to and connivent with the sepals; lip broadly attached to the column, forming a basal nectar cavity, exceeding the other perianth parts, trilobed, the sidelobes basal, erect and partially enfolding the column, with a fleshy, glabrous, bilobed callus fused with and partially forming the nectary front wall. Column short, with 2, short, bilobed, extrorse stigmatic arms at the column apex, the base without a foot; stigmatic cavity immediately below the long, forked rostellum, narrow, perpendicular to the column axis; clinandrium truncate; anther terminal, operculate, incumbent, 1-celled; anther cap oblong in outline, hinged; pollinarium with 2 waxy, dorsoventrally flattened pollinia, attached into 2 depressions on the stipe head by abundant, irregularly shaped viscin (caudicles); viscidium elongate, nearly as long as the stipe, bilobed, the proximal much smaller; stipe long, narrow, somewhat inflated in the middle, somewhat tubularized, the head narrow, with two depressions. Capsules deltoid, weakly carinate, with a short beak and persistent perianth. Seedlings psygmoid and pseudobulbless; pseudobulbs developing at maturity, usually at the end of the first season of growth.

Hybochilus inconspicuus (Kränzlin) Schltr., Repert. Spec. Nov. Regni Veg. 16: 430. 1920. *Rodriguezia inconspicua* Kränzlin, Bull. Herb. Boissier 3: 630. 1895.—TYPE: COSTA RICA. San José Prov., "from the Botanical Institute," without specific locality, fl, *Tonduz s.n.* (holotype: G!).

Rodriguezia candelariae Kränzlin, Bot. Jahrb. Syst. 54, Beibl. 117: 32. 1916.—TYPE: COSTA RICA. San José Prov., Candelaria-Gebirge, *Hoffmann s.n.* (holotype: B, destroyed).

Leochilus parviflorus Standley & L. O. Williams, Ceiba 1: 235. 1951.—TYPE: COSTA RICA. Alajuela Prov., Carrizal, 1500 m, fl, 12 March 1950, *Leon 2325* (holotype: US, photo!; isotype: MO!).

Epiphytic herbs up to 10 cm tall, often blooming at small sizes. Pseudobulbs prominent, suborbicular to oval in outline, wrinkled at maturity, 0.8–2.8 cm tall, 0.7–1.2 cm wide. Leaves 1, rarely 2 per pseudobulb, elliptic-lanceolate, 3.5–9.0 cm long, 0.8–1.8 cm wide. Inflorescences 1, 2, or rarely more, erect to pendent, produced on a mature growth, 6.0–40.0 cm long, bearing 30–150 minute flowers, each node and peduncle covered by a bract, those on nodes 5–17 mm long, those on peduncles 2–3 mm long, often with partially developed or aborted lateral

branches in the proximal 3–5 nodes. Pedicellate ovaries 3–4 mm long. No fragrance detected. Dorsal sepal free, laterals fused up to $\frac{3}{4}$ their length, green-cream with red to red-purple suffused margins, 2.5–3.0 mm long, 1.5–2.0 mm wide. Petals whitish with red-purple margins, 2.5–3.0 mm long, 2.0 mm wide; lip whitish, with a green-yellow spot and red to red-purple maculations in front of the callus, trilobed, the midlobe somewhat concave, retuse, 3.5–5.0 mm long, 1.5–2.0 mm wide; nectary glabrous with high walls; lip callus a deeply bilobed, elongate pad, higher near nectary, covering $\frac{1}{2}$ of lip lamina, glabrous. Column whitish, 0.5–1.0 mm long, 1.0 mm in diameter; anther cap cream; pollinia yellow; stipe elongate with a wedged apex; viscidium golden-brown with a raised center ridge. Capsule carinate, shortly beaked, 1.0–1.5 cm long (including beak), 0.5–1.0 cm in diameter. Fig. 15.

Phenology. Flowering occurs from January through June but is concentrated in February–March. The fruits appear to mature rapidly, and dehiscing capsules occur on plants collected as early as May. These surely represent the fruits set that same year and not those of the previous season because no new sympodium is evident as one would expect if the fruits took one year to mature [the latter is the pattern observed in those species of *Leochilus*, such as *L. crocodiliceps* Reichb.f. and *L. tricuspidatus* (Reichb. f.) Kränzlin, that require twelve months to mature].

Habitat. *Hybochilus inconspicuus* grows on twigs and small branches in cloud forest regions of 1000 to 1500 m. It often occurs on introduced and cultivated plants, on which it may be locally abundant.

Distribution. This species is largely confined to the mountains surrounding the Central Valley of Costa Rica (Fig. 16). This is the same general range exhibited by *Leochilus tricuspidatus*, a species once collected in western Panama; *H. inconspicuus* has been found there as well (Dressler & N. H. Williams, pers. comm.).

REPRESENTATIVE SPECIMENS. COSTA RICA. Alajuela: Naranjo, orilla del Río Colorado, 925–950 m, fl, 7 Apr 1921, *Brenes 11* (AMES, NY); near San Ramón, fl, Jul 1941, *Brenes 23212a* (NY); Carrizal (purch. from street vendor in San José), fl, 23 Feb 1984, *Chase 84305* (CR, MICH). San José: Vicinity of San José, sterile (mixed collection of *H. inconspicuus* and *Leochilus labiatus*), Feb 1924 (AMES); orillas del Río Virilla, entre Heredia y San José, fl, Jun 1931, *Brenes 14299a* (NY); Río Tirribí, near San José, fl, 10 Feb 1924, *Alfaro 33966* (AMES); vicinity of La Verbena, 1200 m, fl, 29 Jan 1924, *Standley 32246* (AMES). Cartago: El Muñeco, S of Navarro, fl, 8–9 Feb 1924, *Standley 33706* (AMES).

This species is difficult to confuse with any other. The combination of a compound panicle, minute, distantly spaced flowers, and a short, complicated column immediately identify it. In Central America, only *Trizeuxis falcata* Lindley has similar small flowers, but they are densely packed (almost into heads), and the plant is psygmoid and lacks well-developed pseudobulbs. *Konantzia minutiflora* Dodson & N. H. Williams from Ecuador is also similar but has an elongate, wingless column and an aborted apical leaf.

Rodriguezia candelariae (for which no type exists) was described by Kränzlin as distinct from *R. inconspicua* on the basis of a smaller flower, a pendent inflorescence, and the presence of abortive lateral branches positioned at the lower lateral buds. Interestingly, he stated that the flowers of this new species were 4 mm long, whereas the length he gave for *R. inconspicua* was 3 mm. The inflorescence habit appears to be variable among plants in the same population, and the

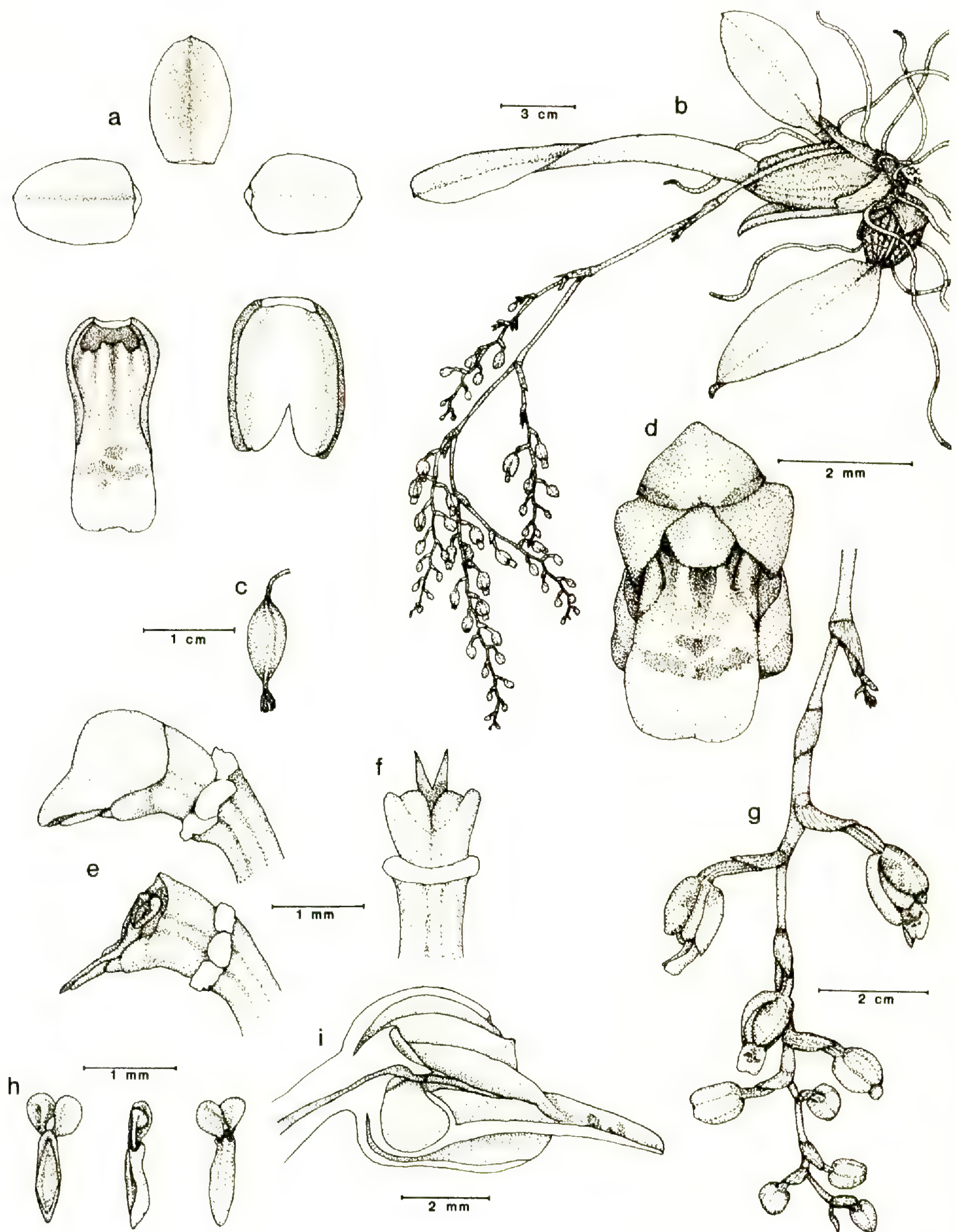


FIG. 15. *Hybochilus inconspicuus*, Costa Rica (MWC84308). a. Perianth parts. b. Habit. c. Capsule. d. Flower, front view. e. Column, side views; with anther cap (top) and with anther cap removed (bottom). f. Column, ventral view. g. Inflorescence habit. h. Pollinarium, three views (l. to r.): abaxial, side, and adaxial. i. Flower, longitudinal section.

abortive lateral branches occur on almost all specimens. Therefore, I consider this to be a typical variant of the earlier concept. Schlechter, who examined Kränzlin's original material, reached the same conclusion (1920).

In the original description of *R. inconspicua*, Kränzlin listed as a synonym *Trichocentrum candidum* Lindley, which was based on material from Guatemala.

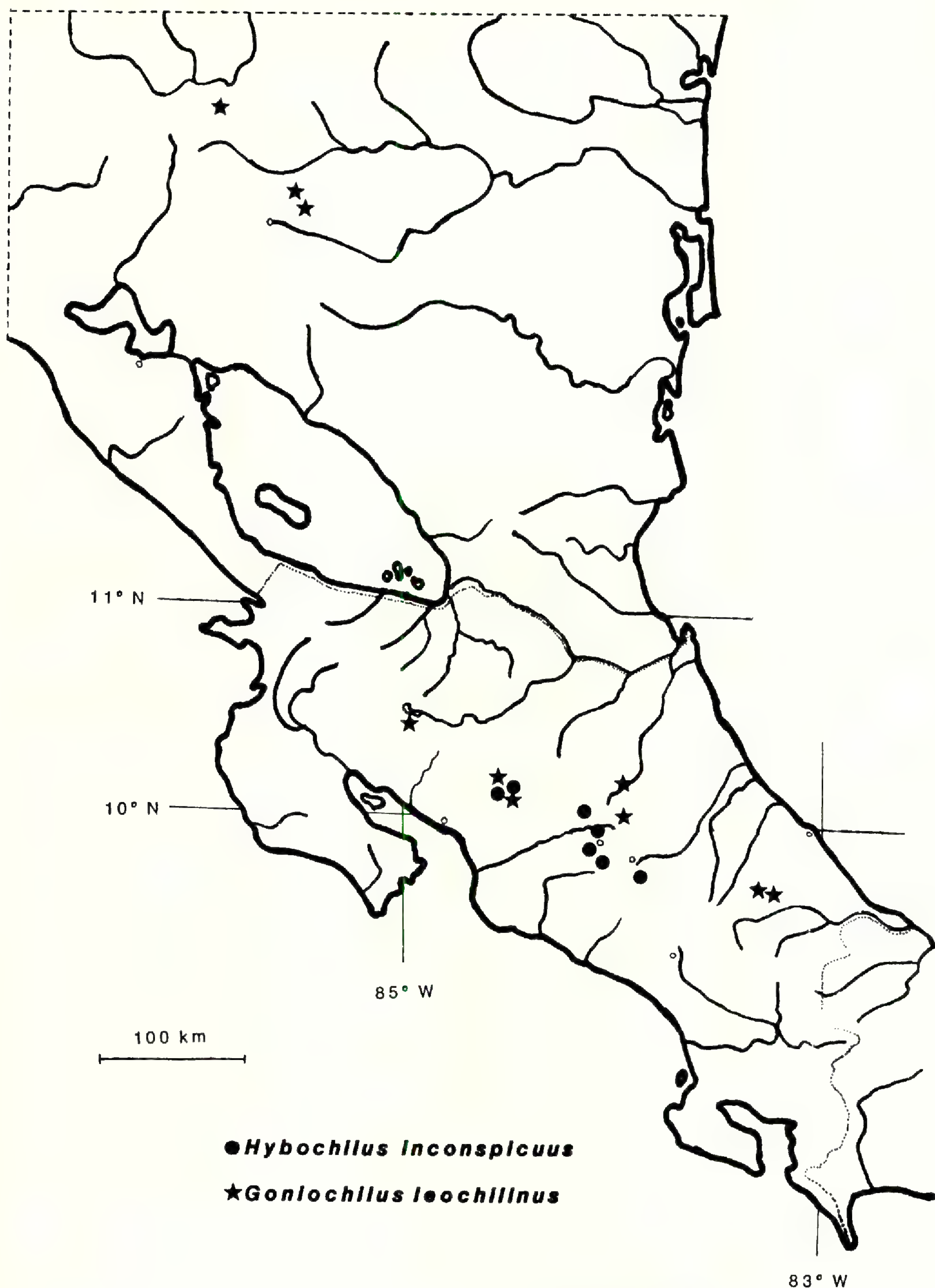


FIG. 16. Distribution of *Hybochilus inconspicuus* and *Goniochilus leochilinus* in southern Central America (southern Nicaragua, Costa Rica, and western Panama).

He stated that, in spite of two discrepancies (which he explained away), Lindley's concept was surely the same as his. He could not, of course, transfer the epithet to *Rodriguezia* because *candida* was already occupied in that genus, and so he gave the species a new name with a new type (the type of *T. candidum* is in the

Lindley Herbarium). This species is not at all similar to Kränzlin's *R. inconspicua* and is a member of *Trichocentrum*, even though it does lack the elongate spur that occurs in most species of that genus.

The epithet *inconspicua* undoubtedly refers to the remarkably small flowers of this species. In Central America, only *Trizeuxis falcata* among the oncidoid species is as small, but a number of genera in South America (*Capanemia*, *Konantzia*, *Quekettia*, among others) have flowers as small or smaller.

Goniochilus M. W. Chase, gen. nov.—TYPE: *Goniochilus leochilinus* (Reichb. f.) M. W. Chase.

Planta epiphytica parvaque habitu *Leochili labiati* (Sw.) Kuntze et pseudobulbis ovoideis et apicaliter unifoliatis. Folia crassa carnosaque. Inflorescentia lateralis, pendula, racemosa vel rarerer paniculata. Flores cernui. Labellum trilobum, nectario basali et apice perpendiculariter flexo. Columna apoda duobus brachiis stigmaticis et anthero semidorsali. Pollinia duo. Stipes amplificatus apicaliter. Viscidium bipartitum.

Small to medium-sized, short-lived, perennial, caespitose herbs, epiphytic on small branches and twigs, with pseudobulbs clustered on short, creeping rhizomes. Pseudobulbs ovoid to suborbicular, ancipitous, unifoliate, lower portions concealed by 2 to 3 sheathing leaves, uppermost larger, eventually deciduous. Leaves elliptic-lanceolate, coriaceous, glabrous, conduplicate, with an unequally bilobed apex, margins entire, eventually deciduous. Inflorescences produced from base of pseudobulb, rarely apically, subtended by a sheathing leaf, moderate to long (for the size of the plant), primarily racemose to weakly paniculate, often secondarily paniculate, pendent, many-flowered. Pedicellate ovaries glabrous, not twisted. Flowers small, weakly colored, inconspicuous, pendent. Lateral sepals free to united up to $\frac{2}{3}$ their length, shortly adnate to the lip base, all sepals subequal, elliptic, dorsally carinate, shortly acuminate to obtuse. Petals free, smaller than sepals, narrowly ovate to oblanceolate, obtuse, forward projecting, concealing column; lip broadly attached to base of column, forming a nectar-secreting cavity, greatly exceeding other perianth parts, trilobed above the middle and bent at a 90° angle to the base, the lip exclusive of the nectary glabrous. Column moderately long, with 2 extrorse stigmatic arms near the anther, the base without a foot; stigma a simple more or less circular cavity; clinandrium truncate, with a prominent protuberance under the stipe; another more or less dorsally situated, operculate, incumbent, 1-celled; anther cap oblong in outline, unhinged; pollinarium with 2 waxy pollinia, with a curving suture on the abaxial side, attached to 2 lateral depressions in the stipe head with abundant, irregularly shaped viscin (caudicles); viscidium oval, distinctly biparted, the stipe with undercurled edges, with a cupshaped, much broadened head and a prominent dorsal protuberance. Capsules deltoid, weakly carinate, with a pronounced beak and persistent perianth. Seedlings psygmoid and pseudobulbless; pseudobulbs developing at maturity, often at the end of the first season of growth.

The genus is named in reference to the lip with the apical half bent at a 90° angle relative to the basal portion.

Goniochilus leochilinus (Reichb. f.) M. W. Chase, comb. nov. *Rodriguezia leochilina* Reichb. f., Gard. Chron. 1: 970. 1871. *Mesospinidium leochilinum* (Reichb. f.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 253. 1923. *Hybochilus leochilinus* (Reichb. f.) Mansf., Repert. Spec. Nov. Regni Veg. 44: 58. 1938.—TYPE: COSTA RICA. Without specific locality, collector unknown, “flowered in the Royal Exotic Nursery of Messrs. Veitch & Sons” (holotype: W!).

Epiphytic herbs up to 15 cm tall, often blooming at small sizes in the first year of growth, typically red-purple suffused throughout. Pseudobulbs usually prominent, strongly ancipitous, suborbicular to oval in outline, 0.6–2.0 cm tall, 1.0–1.5 cm wide. Leaves nearly always 1 per pseudobulb, narrowly elliptic-lanceolate, 2.5–14.0 cm long, 0.6–2.4 cm wide, with a well-developed conduplicate petiole. Inflorescences 1, 2, or rarely more, weak, pendent, produced on a mature growth, zigzag, 7.0–45.0 cm long, bearing 5–60 flowers, each node and peduncle covered by a bract 3–12 mm long, those covering lateral buds much larger. Pedicellate ovaries 4–6 mm long. Flowers sweetly fragrant. Dorsal sepal free, lateral sepals free to fused up to $\frac{2}{3}$ their length, green-yellow, with large red-brown to brown maculations, 6–9 mm long, 4–5 mm wide. Petals similar, 5–8 mm long, 3–4 mm wide; lip white with red to rose-red spots in front of the callus, midlobe subquadrate, convex, retuse, side lobes broadly triangular, whole lip 10–13 mm long, 4–6 mm wide across the lateral lobes; nectary shallow with a densely pilose throat; lip callus a raised rectangular, sulcate pad, higher toward the lip base, situated much in front of the nectary, more or less glabrous to slightly papillose. Column whitish with red markings, 5–7 mm long, 1–2 mm in diameter; anther cap cream; pollinia yellow, ovoid. Capsule weakly carinate with an elongate beak, 3.0–4.5 cm long (including beak), 1.0–1.5 cm in diameter. Fig. 17.

Phenology. Flowering in *Goniochilus leochilinus* occurs from late September to early January, but is concentrated in October and November. Fruit maturation appears to take ten to twelve months, and dehiscence takes places shortly before the next season's flowering.

Habitat. This species grows on twigs and other smaller branches of woody plants in cloud and rain forests. Its elevational range is from 500 to 1500 m. As is true of most twig epiphytes, *G. leochilinus* moves onto introduced and cultivated plants, especially *Citrus*, *Coffea*, and *Psidium guajava*, on which it may be locally abundant.

Distribution. This species has been collected in the Cordillera Central and the Atlantic watershed of Costa Rica and Nicaragua (Fig. 16). It also has been reported from western Panama (Dressler & N. H. Williams, pers. comm.).

REPRESENTATIVE SPECIMENS. NICARAGUA. Jinotega: Jinotega Grande, 1350 m, fl, *Heller 4232* (SEL). Matagalpa: Finca El Roblar, 850 m, fl, *Heller 3977* (SEL); Cordillera Central de Nicaragua, 4–6 km N of Santa María de Ostuma, 1500–1600 m, fl, 28 Nov 1973, *Williams & Molina R. 42517* (F); Finca La Harmonía, 1300 m, fl, *Heller 3308* (SEL).—COSTA RICA: Guanacaste: Los Ayotes, near Tilarán, 600–700 m, sterile, 21 Jan 1926, *Standley & Valerio 45438* (AMES). Alajuela: San Pedro de San Ramón, 1200 m, fl, June 1921 (AMES), and Cerro de San Rafael de San Ramón, 1275 m, fl, 25 Nov 1921 (NY), *Brenes 193*; San Isidro de San Ramón, 1050 m, fl, 12 Nov 1923, *Brenes 2992* (NY); 20 km from San Ramón exit off Interamerican Hwy on rd to La Paz, 84°34'W, 10°10'N, 1200 m, fr, 19 Mar 1984, *Chase 84371* (CR, MICH); Virgen del Socorro, 800 m, fl (buds only), 15 Sept 1979, *Luer, Luer, & Walter 4173a* (SEL). San José: beside Río La Hondura, 1050 m, fl, early fr, 5 Dec 1971, *Lent 2285* (AMES, F, MO). Limón: lago sin nombre al pie de Fila Lleskila, 1160 m, fl, 4 Nov 1984, *Gómez*

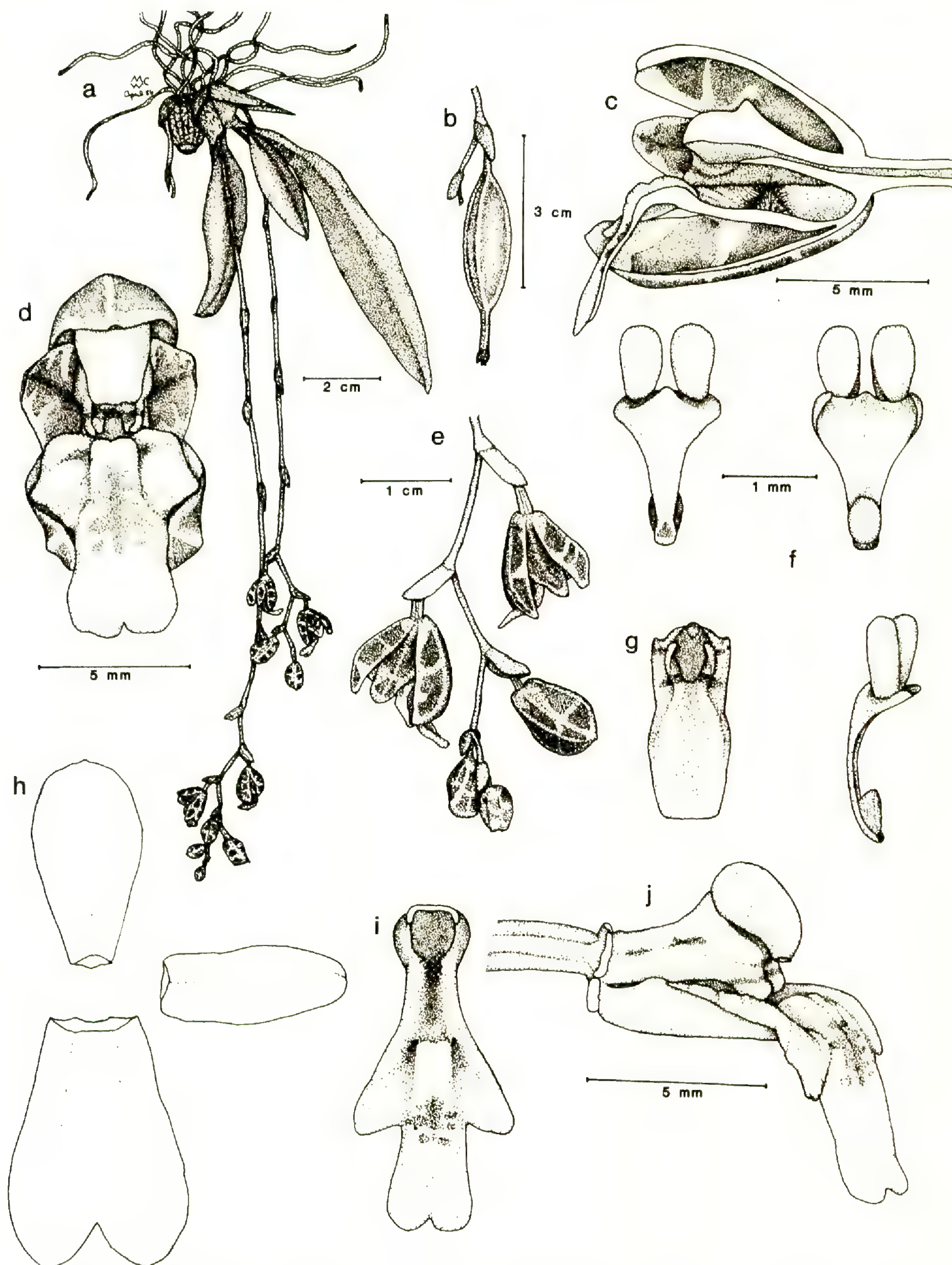


FIG. 17. *Goniochilus leochilinus*, Costa Rica (MWC84210). a. Habit. b. Capsule. c. Flower, longitudinal section. d. Flower, front view. e. Inflorescence habit. f. Pollinarium, three views: top, adaxial (l.) and abaxial (r.); bottom, side. g. Column (with anther cap removed), ventral view. h. Perianth outlines (exclusive of lip). i. Lip (flattened). j. Column and lip, side view (with sepals and petals removed).

et al. 23105 (MO); entre Dabagri y Sacabico y los bordes del mismo, fl, 7 Nov 1984, Gómez *et al.* 23301 (MO).

This species is easily distinguished by its red-purple suffused plants with weak, pendent inflorescences, pendent flowers, a trilobed lip bent in the middle, and a

basal hornless nectary. No other oncioid species could be confused with this distinctive plant.

After the type collection of *G. leochilinus* was made (it was described in 1871), it was not recollected until 1920, after which time it has been regularly encountered. My general impression is that it is much more common than the number of collections indicates. It is easily overlooked and grows on common plants where collectors are unlikely to search. Heller (personal notes at SEL) indicated that he frequently encountered the species in Nicaragua.

The species epithet means "smooth lip," an apparent reference to the lack of a complex, tuberculate, lip callus. On the type sheet in the Reichenbach Herbarium, this name appears after a crossed out one, "pantherina." Evidently, Reichenbach had originally given it this name, which would refer to the large, brown maculations of the perianth, and then changed his mind.

EXCLUDED NAME

Hybochilus huebneri Mansf., Repert. Spec. Nov. Regni Veg. 36: 61. 1934.—

TYPE: COLOMBIA. Vaupés, Río Negro Basin, El Castillo, near confluences of Guainía and Casiquiare, fl, 12 Dec 1942, *Schultes & López 9300* (neotype: AMES!). = *Polyotidium huebneri* (Mansf.) Garay, Bot. Mus. Leaf. 18: 105. 1958.

ACKNOWLEDGMENTS

I thank William R. Anderson and Leslie A. Garay for their assistance. I am also grateful to the curators of the herbaria that loaned specimens, in particular those of Vienna and Geneva, who were kind enough to send me the Reichenbach and Kränzlin types. The live material was collected during my field research on *Leochilus*; this work was supported by NSF Grant BSR83-00786 to the University of Michigan. The scanning electron microscope used in this work was acquired under NSF Grant BSR83-14092 to the University of Michigan.

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NEW SPECIES OF ECHEANDIA (LILIACEAE) FROM NUEVA GALICIA

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The following species are proposed to provide names for the *Flora Novo-Galiciana*. I thank the curators of the following herbaria for the opportunity to examine material from their collections: ARIZ, ASU, BM, DS, ENCB, F, GH, K, LL, MEXU, MICH, MO, NA, NY, TEX, U, UC, US, WIS.

Echeandia mcvaughii Cruden, sp. nov.—TYPE: MEXICO. Jalisco: Ruta 15, ca 4 km NE junction Ruta 80, ca 30 km SW Guadalajara, 1600 m, 11 Aug 1968, *Cruden 1502* (holotype: UC; isotypes: ENCB, F, GH, K, MEXU, MICH, MO, NY, TEX, US, WIS).

Radicitubera ab cormo 0.5–3 cm. Scapus glaber vel scaber, saepe scaber prope basin super glaber, 0.3–1.2 m altus. Folia basalia 5–10. Tepala alba, anguste elliptica. Filamenta clavata, squamosa. Antherae connatae, conus gracilis. Capsula subglobosa.

Root-tubers 0.5–3 cm from corm, 1.5–3 cm long. Scape glabrous to scabrous, frequently scabrous near the base and glabrous above, 0.3–1.2 m high. Basal leaves 5–10, narrowly ovate to narrowly obovate, frequently falcate, 10–40 cm long, 10–30 mm wide, (entire) denticulate to ciliate. Cauline leaves (0–) 1–4, reduced to bracts. Flowers white, opening in the afternoon. Tepals 10–17 mm long, inner 2–3 mm wide, outer 1.5–2 mm wide. Filaments clavate, scaled, 2.5–4 mm long. Anthers connate, 6–11 mm long, usually more than twice the length of the filaments, cone long and slender, not strongly tapered, diameter at insertion of filaments rarely twice that of the apex, (0.9–) 1.0–1.6 (–1.8) mm wide at insertion of filaments, (0.5–) 0.6–1.0 (–1.2) mm wide at apex. Capsules globose to subglobose, 4–7 mm long, 4–6 mm wide. In flower July–August. Chromosome number $n = 8$ (*Cruden 1502, 1676, 1823, 1872*).

REPRESENTATIVE SPECIMENS: MEXICO. Jalisco: Ruta 15, ca 24 km W Guadalajara, ca 1600 m, *Cruden 1872* (GH, K, MEXU, MO, UC); Ruta 80, just E Acatlán, 1450 m, *Cruden 1676* (ENCB, UC); ca 5 rd mi SW Santa Cruz de las Flores, 1550 m, *McVaugh 16300* (MICH). Nayarit: Ruta 15, ca 26 km NW Tepic, *Cruden 1051* (ENCB, F, GH, K, UC, US); Ruta 15, K157–158, ca 18.5 km NW Ixtlán del Río, ca 900 m, *Cruden 1823* (ASU, ENCB, F, GH, K, MEXU, MO, NY, TEX, UC, US); SW Santa María del Oro, *Gentry 11018* (LL, MEXU, MICH); nr Tetitlán, ca 15 km W Ahuacatlán, 900–1000 m, *Feddema 503* (MICH).

This species is found in tropical deciduous forest, oak woods, subtropical scrub, and grasslands between 750 and 1600 m in a narrow region from northwest of Tepic to southwest of Guadalajara. It is distinguished by the large, clustered tubers, relative broad, usually falcate leaves, and a slender anther cone that is usually more than twice the length of the scaled filaments.

This handsome, endemic species is named for Rogers McVaugh, student of the flora of Nueva Galicia.

Echeandia parvicapsulata Cruden, sp. nov.—TYPE: MEXICO. Jalisco: Ruta 80, at top of pass ca 5 km SW La Huerta, ca 500 m, 15 Sep 1971, *Cruden 1987* (holotype: UC; isotypes: ENCB, GH, K, MO).

Radicitubera ab cormo 2–5 cm. Scapus glaber, 25–89 cm altus. Folia basalia 4–8, angusta. Folia caulina 2–6. Tepala alba, anguste elliptica. Filamenta anguste cylindrica, glabra. Antherae connatae. Capsula globosa vel late oblonga, 2.5–4 mm longa.

Root-tubers 2–5 cm from corm, 1–2 cm long. Scape glabrous, (25–) 55–89 cm high. Basal leaves 4–8, narrowly obovate, (14–) 22–65 cm long, 6–13 (–15) mm wide, entire to short ciliate. Cauline leaves 2–6, reduced to bracts, lowest to 8.5 cm long in robust specimens. Flowers white, opening in late afternoon. Tepals 9–10 mm long, inner 1.2–2.5 mm wide, outer 1–1.5 mm wide. Filaments narrowly cylindric, glabrous, 3.5–4 mm long. Anthers connate, cone strongly tapered, 5.5–6.5 mm long. Ovaries 1.9–2.2 mm long. Capsules globose to broadly oblong, 2.5–4 mm long, 2.5–3.5 wide. In flower August–September. Chromosome number $n = 8$ (*Cruden 1987, 2062*).

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Jalisco: 3 mi S La Huerta, 500–550 m, *McVaugh 19812* (MICH); 11 mi N of bridge of Río Cihuatlán on road from Santiago, Colima to Durazno, Jal., 500–550 m, *McVaugh 15947* (MICH). Nayarit: Ruta 200, 46–47 km W Compostela, ca 300 m, (flowered in greenhouse Jul 1974), *Cruden 2062* (MEXU, UC); 1.5 mi W Mazatán, rd to Las Varas, ca 600 m, *Feddema 1130* (MICH).

This species is found between 300 and 600 m in oak woods. It might be confused with *E. parviflora*, which has scabrous stems, at least near the base, ciliate leaf margins, and is generally associated with tropical deciduous forest.

Echeandia coalcomanensis Cruden, sp. nov.—TYPE: MEXICO. Michoacán: Dist. Coalcomán, Pto. Zarzamora, 3 Aug 1939, *Hinton et al. 15034* (holotype: GH; isotypes: ARIZ, LL, NY–2 sheets, US).

Radicitubera juxta cormum. Scapus glaber, usque ad 82 cm altus. Folia basalia 3–5. Folium caulinum 1, nonbracteatum, folium basale simulans, si 2 nunc superius bracteatum. Tepala alba, anguste elliptica. Filamenta anguste clavata, squamata. Antherae connatae.

Root-tubers 0.5–1.5 cm from corm, 1–3 cm long, Scape glabrous, 59–82 cm high. Basal leaves 3–5, narrowly obovate, 35–45 cm long, 5–14 mm wide, serrulate to denticulate. Cauline leaves 1 (–2), quite long and similar to basal leaves, if 2 the upper bractlike. Flowers white, pendulous. Tepals 9–11 mm long, to 2 mm wide. Filaments narrowly clavate, scaled, 2.5–4.5 mm long. Anthers 5.5–8 mm long, ca twice the length of the filaments, cone strongly tapered, diameter 1.5–2.3 mm wide near the insertion of the filaments, 0.3–0.6 mm wide at apex. Ovaries 1–2 mm long. Fruits not seen.

In general aspect both *E. mexicana*, which has yellow flowers and broader tepals, and *E. gentryi*, which has free anthers, resemble this species.

Echeandia sinaloensis Cruden, sp. nov.—TYPE: MEXICO. Sinaloa: Mazatlán, Jul 1934, *Ortega 7277* (holotype: UC; isotypes: F, K, US).

Radicitubera ab cormo 1–2.5 cm. Scapus scaber, 15–50 cm altus. Folia basalia 6–14. Folia caulina 1–2. Tepala alba, anguste elliptica. Filamenta anguste cylindrica, glabra. Antherae connatae, filamentis 2–3plo longiores. Capsula globosa, parva.

Root-tubers 1–2.5 cm from corm, ca 1 cm long. Scape scabrous, 15–50 cm high. Basal leaves 6–14, narrowly obovate, 5–25 cm long, 2–8 mm wide, entire to denticulate. Cauline leaves 1–2, reduced to bracts. Flowers white. Tepals 8.5–10 mm long, 1–2 mm wide. Filaments narrowly cylindric, glabrous, sometimes twisted and appearing scaled, 1.5–2.5 cm long. Anthers connate, 4–6.5 mm long, 2 or more times the length of the filaments, diameter of cone at insertion of filaments more than twice that of apex. Ovaries 1–1.5 mm long. Capsules globose, 3.5–4 mm long. In flower July–August.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Jalisco: 65 km NW Chamela, 11 km N rd to Tomatlán, *Pérez* 745 (MEXU). Sinaloa: *Ortega* 6347 (DS, GH, US); N Mazatlán, 5–20 m, *Pennell* 19742 (US); between Rosaria and Colomos, *Rose* 1622 (US); San Ignacio, *Ortega* 4034 (MEXU).

This diminutive species is found in lowland tropical forests. The numerous leaves, small flowers with long anthers, scabrous scape, and tiny root-tubers are distinctive.

Echeandia pihuamensis Cruden, sp. nov.—TYPE: MEXICO. Jalisco: Ruta 110, ca K178, ca 10.5 km SW Pihuamo, roadside with *Mimosa*, *Oxalis*, ca 725 m, 2 Jul 1968, *Cruden* 1330 (holotype: UC; isotypes: ENCB, F, GH, K, MEXU, MICH, MO, NY, US).

Radicitubera ab cormo 0.5–3 cm. Scapus glaber, 20–50 cm altus. Folia basalia 5–8. Folia caulina 0–1. Tepala alba, anguste elliptica. Filamenta anguste cylindrica, glabra. Antherae liberae, ab imo ad summum angustatae.

Root-tubers 0.5–3 cm from corm, 1–1.5 cm long. Scape glabrous, 20–50 cm high. Basal leaves 5–8, linear, 12–40 cm long, 4–10 mm wide, entire to denticulate. Cauline leaves 0–1, when present reduced to a bract. Tepals white, 6–8 mm long, 1–1.5 mm wide. Filaments narrowly cylindric, glabrous, 2.5–3 mm long. Anthers free, 2.5–3.5 mm long, bases flared, tapered from base to apex. Ovaries 1.5–2 mm long. In flower July. Chromosome number $n = 8$ (*Cruden* 1330).

Echeandia robusta Cruden, sp. nov.—TYPE: MEXICO. Jalisco: Ruta 80, ca K176, ca 15 km SW Autlán, steep bank and oak woods with *Calliandra*, *Cuphea*, *Commelina*, *Dahlia*, ca 970 m, 15 Sep 1971, *Cruden* 1990 (holotype: UC; isotypes: ENCB, GH, K, MEXU, MO).

Radicitubera ab cormo 1–3 cm. Scapus glaber, 1.1–1.8 m altus. Folia basalia 4–6, lata. Folia caulina alba, 7–11. Tepala alba. Filamenta anguste cylindrica, squamosa. Antherae liberae. Capsula oblonga.

Root-tubers 1–3 cm from corm, 1–2.5 cm long. Scape glabrous, 1.1–1.8 m high. Basal leaves 4–6, narrowly obovate, 38–75 cm long, 29–60 mm wide, entire. Cauline leaves 7–11, white, lowest to 43 cm long. Flowers white, opening in afternoon. Tepals narrowly elliptic, spreading, 11–15 mm long, inner 3.5–4.5 mm wide, outer 2.5–3.5 mm wide. Filaments narrowly cylindric, scaled, 5–6 mm long. Anthers free, dehiscing apically, 4.5–6 mm long. Capsules oblong, 11 mm long, 5 mm wide. In flower September–October. Chromosome number $n = 8$ (*Cruden* 1990).

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Jalisco: topotype, *McVaugh* 19890 (MICH). Michoacán: Dist. Coalcomán, *Aquila*, *Hinton et al.* 16162 (US).

This species is distinguished by its robust vegetative stature, broad basal leaves, many cauline leaves, tubers close to the corm, and anthers that dehisce through apical slits. The flowers resemble those of *E. echeandioides*, which are yellow and open in the morning.

Echeandia gentryi Cruden, sp. nov.—TYPE: MEXICO. Sinaloa: Ocurahui, Sierra Surotato, 6000–7000 ft, 1–10 Sep 1941, *Gentry 6254* (holotype: MICH; isotypes: ARIZ, GH, MO, NY).

Radicitubera juxta cormum. Scapus glaber, 30–61 cm altus. Folia basalia 3–8, angusta. Folia caulina 1–2. Tepala alba, anguste elliptica. Filamenta anguste cylindrica, squamosa. Antherae liberae.

Root-tubers next to the corm, 1–2 cm long. Scape glabrous, 30–61 cm high. Basal leaves 3–8, linear, 16–40 cm long, 0.5–6 mm wide, entire to short ciliate. Cauline leaves 1–2, reduced to bracts. Tepals white, 8–13 mm long, inner 2.5–5 mm wide, outer 1–2.5 mm wide. Filaments narrowly cylindric, scaled, 3.5–5.5 mm long. Anthers free, 2–4.5 mm long. Ovaries 1.8–2.5 mm long. In flower July–September.

ADDITIONAL SPECIMENS EXAMINED: MEXICO. Durango: 3 mi NE Otinapa, 2300–2400 m, *Maysilles 7329* (MICH). Nayarit: nr Cangrejo, ca 3 mi W Mesa del Nayar, *Norris & Taranto 14684* (MICH); ca 4 mi E La Ciénaga, ca 5 mi NW Mesa del Nayar, *Norris & Taranto 14244* (MICH).

This is a species of pine and pine-oak forests of middle elevations in the Sierra Madre Occidental. Its closest relatives are probably *E. coalcomanensis* and an undescribed species from Oaxaca.

Echeandia udipratensis Cruden, sp. nov. TYPE: MEXICO. Jalisco: Ruta 110, K43–44 [just N of Mazamitla], ca 4.5 km S Michoacán-Jalisco border, ca 2120 m, 2 July 1968, *Cruden 1329* (holotype: UC; isotypes: GH, K, MEXU, MO).

Radicitubera juxta cormum. Scapus glaber, 53–112 cm altus. Folia basalia 4–6, lata, ciliata. Folia caulina 2–3. Tepala flava, elliptica. Filamenta anguste clavata, squamata. Antherae liberae. Capsula oblonga.

Root-tubers close to corm, 3–5 cm long. Stem glabrous, 53–73 cm long in early flower, to 112 cm high in fruit. Basal leaves 4–6, ciliate, narrowly obovate, 25–50 cm long, 18–28 mm wide. Cauline leaves 2–3, reduced to broad bracts which encircle the stem, lower 4–7.5 cm long. Tepals yellow, elliptical, 16–19 mm long, inner 8–10 mm wide, outer 4–7.5 mm wide. Filaments 8–9.5 mm long, narrowly clavate, strongly scaled. Anthers free, versatile, 3–4 mm long. Ovaries 3.5–5.4 mm long. Capsules oblong, 13–16 mm long, 5.5–6.5 mm wide. In flower July. Chromosome number $n = 40$ (*Cruden 1329*).

ADDITIONAL SPECIMEN EXAMINED: MEXICO. Jalisco: Sierra del Tigre, 2 mi NE Mazamitla, 2100 m, 23 Sep 1952, *McVaugh 13181* (MICH).

Both collection sites are described as wet, meadowlike areas in an area of pine forest. The combination of large flowers and capsules, clustered tubers, and broad ciliate leaves are distinctive.

Echeandia occidentalis Cruden, sp. nov.—TYPE: MEXICO. Nayarit: Ruta 15, K190–191, ca 39 km SE Tepic, ca 1250 m, 16 Sep 1971, *Cruden 1994* (holotype: UC; isotypes: GH, K, MEXU, US).

Radicitubera juxta cormum. Scapus glaber, 60–135 cm altus. Folia basalia (4–) 5–11. Folia caulina 2–7 (–11). Tepala flava, elliptica. Filamenta anguste cylindrica vel anguste clavata, squamosa. Antherae connatae.

Root-tubers close to the corm, 2–5 (–8) cm long. Scapes 60–135 cm high, glabrous. Basal leaves (4–) 5–11, narrowly ovate to narrowly obovate, attenuate, 29–80 cm long, 5–15 (–25) cm wide, entire, denticulate or serrulate. Cauline leaves 2–9 (–11), lower usually well-developed. Flowers yellow to yellow-orange, tepals (12–) 13–19 mm long. Filaments narrowly cylindric (narrowly clavate), scaled, (5–) 5.5–7 mm long. Anthers connate, (5–) 7–10 mm long, mostly 1.5–2 mm longer than filaments, in some populations greenish yellow and contrasting with the yellow-orange filaments, diameter of anther cone at insertion of filaments more than twice that of apex. Ovaries 2.5–4.5 mm long. Capsules 10–14 mm long, 3–4 mm wide. In flower mid-July–September (late October). Chromosome number $n = 8$ (*Cruden 1667, 1882, 1994*).

REPRESENTATIVE SPECIMENS: MEXICO. Jalisco: 16 km SW Pihuamo, ca 790 m, *Cruden 1667* (ENCB, GH, MO, UC); Ruta 80, K171–172, S Autlán, 1250 m, *Cruden 1882* (ENCB, NY, UC); Barranca de Colimilla, ca 4 mi NE Guadalajara, ca 4000 ft, *Gentry & Gilly 10908* (MICH). Michoacán: 21 km S Uruapan, ca 1210 m, *Cruden 1981* (F, K, UC, US). Nayarit: Acaponeta to Pedro Paulo, *Rose 1939* (GH, MICH, MO, NY, UC, US); Cerro San Juan, W Tepic, 1000 m, *Mexia 719* (GH, MICH, MO, NY, US); 9 mi N Compostela, 1000–1200 m, *McVaugh 16486* (MICH); 3.5 mi NW Ahuacatlán, S base Volcán Ceboruco, ca 1100 m, *Feddema 428* (MICH); Yxtlán to San Marcos, 1100 m, *Mexia 858* (BM, F, NA, US).

This species occurs between 850–1300 (–1650) m from Nayarit into western Michoacán, primarily in tropical deciduous forest and oak woods. It usually has more basal and cauline leaves than *E. mexicana*, a species of pine-oak forests at higher elevations.

Echeandia imbricata Cruden, sp. nov.—TYPE: MEXICO. Jalisco: Precipitous south-facing mountain sides, 4 mi NNE Talpa de Allende, oak forest zone, nr road-summit, 1450–1500 m, 12–13 Oct 1960, *McVaugh 20109* (holotype: MICH).

Radicitubera ab cormo 3–6 cm. Scapus glaber, 62–72 cm altus. Folia caulina 8–12, attenuata, imbricata, cinerascens. Tepala flava, elliptica. Filamenta anguste cylindrica, squamata. Antherae liberae.

Root-tubers 3–6 cm from corm, 2–3 cm long. Basal leaves 6–7, linear, $\pm$ falcate, 27–33 cm long, 3–14 mm wide, denticulate-serrulate. Scape glabrous, 62–72 cm high. Cauline leaves 8–12, narrowly ovate, the lower overlapping, sometimes enclosing the scape. Flowers yellow. Tepals 14–16 mm long, 3–5-veined. Filaments narrowly cylindric, scaled, 8–8.5 mm long. Anthers 3–3.5 mm long, dehiscing laterally. Ovaries 2.5–3 mm long. In flower October–November.

ADDITIONAL SPECIMENS EXAMINED. MEXICO. Guerrero: Dist. Adama, Temisco, Cerro de la Guacamaya, 400 m, *Mexia 8840* (F, GH, MO, NY, U, US). Michoacán: Barranca Hondo, rd between Uruapan and Apatzingán, ca 1000 m, *Lape 28* (MICH).

The yellow flowers and long, overlapping cauline leaves distinguish this species from *E. tenuis*, which has white flowers and small, non-overlapping cauline leaves.

SOME LATIN AMERICAN MOSSES NEW TO SCIENCE

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In the course of four decades of intermittent involvement with the mosses of Latin America, I set aside a number of problem specimens, some of them long forgotten. A good number of them ceased to be problems as my knowledge and understanding increased, some exceeded the limits of my patience and were assigned names that would at least make them available for study by others, and a fair number, including those described below, seemed to merit description.

Leptotheca hamiltonii Crum, sp. nov.

Figs. 1–7.

Plantae 4–5 cm altitudine, dense compactae, valde tomentosae, erectae, sparse furcatae. Folia laxe erecta, 2–3 mm longa, oblongo-lanceolata, acuta et aristata, basi decurrentia, marginibus inferne revolutis, superne serratis; costa excurrens, dorse teres, superne parve serrata; cellulae superiores breviter rhomboideae, 1–2:1, laeves, parietibus incrassatis, basiales oblongo-rhomboideae. Propagula in axillis foliorum superiorum aggregata, filamentosa, fusca vel subnigra.

Plants 4–5 cm high, compactly tufted, shiny yellow to greenish yellow, densely matted with a reddish tomentum below. Stems erect, sparsely and irregularly branched. Leaves loosely erect or erect-spreading when dry, somewhat more spreading at stem and branch tips, erect when moist, moderately concave, 2–3 mm long, oblong-lanceolate, decurrent, acute, ending in a short, $\pm$ stout, yellow-green, sparsely serrulate awn; margins recurved in the lower half or more, serrulate above the middle, serrate near the apex; costa excurrent, prominent at back, sparsely serrulate-toothed above; upper cells irregularly rhombic to oblong-rhombic, ca. 1–2:1, thick-walled, smooth, those of the spreading upper leaves oblong-linear, flexuose, gradually longer below, the basal cells oblong-rhomboidal, somewhat shorter at the margins or, in upper leaves, all basal cells sublinear. Inflorescences and sporophytes unknown. Dark brown or blackish, smooth or faintly papillose brood filaments 9–13 cells long produced abundantly on short, branched stalks in axils of upper leaves.

TYPE: PERU. Depto. San Martín, Dist. Pataz, valley of Río Apisoncho, ca. 30 km E of Parcoy, on damp, shaded, rotting branch just above ground, subalpine forest, 1 Aug–15 Sep 1965, A. C. Hamilton & P. M. Holligan 42 (holotype: MICH). The specimen was collected on the Cambridge Botanical Expedition to North Peru.

The species of *Leptotheca* are all similar in overall appearance and leaf structure. This new species from Peru is quite large as compared with the others, and it is particularly distinctive because of its growth in dense clods compacted by a heavy growth of reddish tomentum in the lower half or more. It much resembles a



FIGS. 1-7. *Leptotheca hamiltonii*. 1. Habit, $\times 2$. 2. Leaves, $\times 16$. 3, 4. Cells at leaf apex, $\times 290$. 5. Alar cells, $\times 290$. 6. Brood filaments, $\times 76$. 7. Branch stalk of clustered brood filaments, $\times 290$.

species of *Campylopus* because of its robust stature and considerable development of tomentum. The majority of the leaves are erect and not much incurved or otherwise contorted when dry, and the leaf cells are rhombic or oblong-rhombic, but those at the stem tips are somewhat spreading and have longer cells. The upper leaves commonly subtend dense clusters of dark brown or even blackish brood filaments. The costa ends as a sparsely serrulate awn, and the leaf margins are revolute below and moderately serrate above. In most respects the species is like *L. costaricensis* Card. & Thér. (known from Jamaica, Colombia, and Costa Rica). However, that species is considerably smaller and less tomentose, and its leaves are narrower and more slender-pointed, with the costa strongly toothed at back above and on the awns. Its upper leaves have cells less markedly elongate, and its brood filaments are more distinctly papillose. *Leptotheca boliviana* Herz. differs in much the same ways, but its leaves are erect-incurved when dry, and its brood filaments are shorter and elongate-clavate. *Leptotheca gaudichaudii* (Spreng.) Schwaegr. (of Tierra del Fuego, South Georgia, New Zealand, Australia, and South Africa) has leaf margins usually plane, cells subquadrate throughout, awns stout and entire, and brood filaments sometimes much longer (as many as 30 cells in length). I have no knowledge of *L. wattii* Card. & Thér.

Churchill and Buck (1982) have made *L. costaricensis* a synonym of *L. boliviana*. They recognized *L. gaudichaudii* var. *wattii* but noted that the known specimens are mixtures with the var. *gaudichaudii*.

Breutelia maegdefraui Crum, nom. nov. *Breutelia rhytidioides* Crum ex Mägdefrau, Nova Hedwigia 38: 58. 1983, non *B. rhytidioides* Herz., 1934.

I am indebted to Marshall Crosby for calling my attention to a previous homonym (of a slightly different spelling).

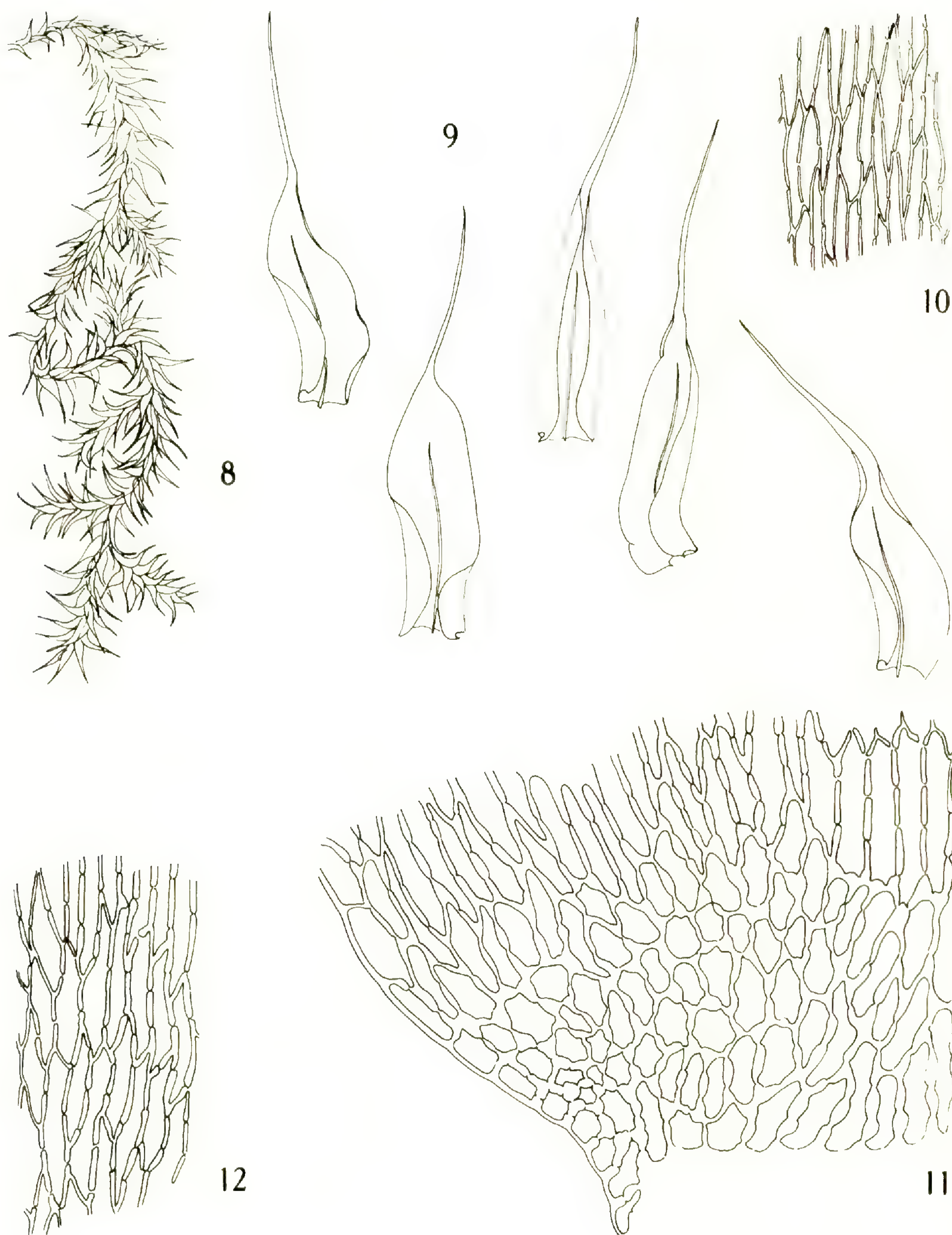
Spiridentopsis longissima (Raddi) Broth.

Figs. 8–12.

Robust plants in loose, moderately shiny, yellow-brown, pendent masses. Stems flexuose, distantly subpinnate. Branches horizontal, subequal. Stem and branch leaves similar, squarrose-spreading, about 5–6 mm long, abruptly narrowed to a long, flat subula (about 3 mm long) from an oblong-ovate, concave base, cordate at the insertion; margins erect, finely serrulate for a short distance below the base of the acumen; costa slender, single, ending about $\frac{2}{3}$ up the leaf; upper cells linear-rhomboidal, relatively thin-walled and moderately porose; cells of leaf base larger, thick-walled, strongly pitted, and golden-yellow across the insertion, those at the basal angles short and irregular with thick, strongly pitted walls, those at the middle of the insertion rather shortly rhomboidal. Apparently dioicous; perichaetia small.

BRAZIL. Paraná: Mun. São José dos Pinhais, road to Guaricana, low area where the electricity wires come near the road, ca. 25°40'S, 49°W, evergreen forest, often misty or rainy, ca. 900–1000 m, hanging, 1 Nov 1977, L. R. Landrum 2328 (MICH; NY).

The plants are quite similar in appearance to a *Zelometeorium* because of short, spreading branches and conspicuously squarrose leaves. They differ significantly, however, in having long-subulate leaf points and porose cells, with those in the alar regions noticeably differentiated in shape and color. I had planned to describe this collection as a new genus and species, perhaps because I had not sufficiently considered a relationship with the Pterobryaceae. The differences be-



FIGS. 8-12. *Spiridentopsis longissima*. 8. Habit, $\times 1$. 9. Leaves, $\times 6$. 10. Upper median cells, $\times 290$. 11. Alar cells, $\times 290$. 12. Cells of upper portion of leaf base, $\times 290$.

tween that family and the Meteoraceae are indeed unconvincing, but a pendent habit of growth may argue for a more reasonable placement in the latter. I am grateful to my friend William Buck for helping me to see my mistake before I made it!

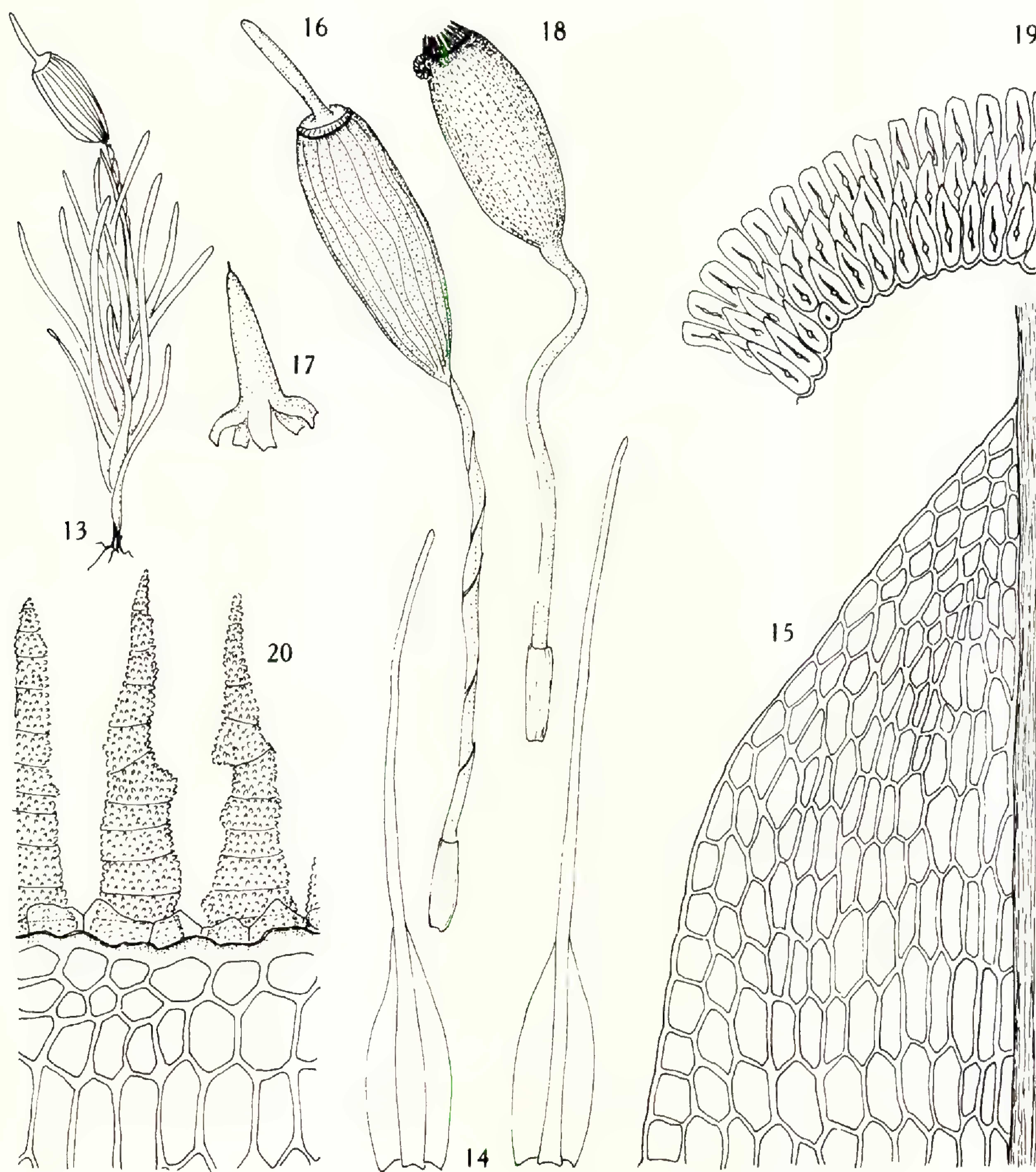
The rarity of the species can be judged by the fact that only two collections are to be seen, otherwise, in the herbarium, both from Serra do Mar, Paraná, both sterile. Brotherus, in *Die natürlichen Pflanzenfamilien* (1925), described the sporophyte but said he had not seen an example.

Brachydontium curvisetum Crum, sp. nov.

Figs. 13–20.

Plantae pusillae, dense caespitosae, usque ad 5 mm altitudine, saepe furcatae. Folia sicca erecto-flexuosa, madida erecta vel plus minusve patentia, 1.5–3 mm longa, subulata e basi oblongo-ovato, marginibus planis integrisque; costa totum subulae occupans; cellulae basis folii oblongae, superne breviter rhomboideae vel subquadratae. Dioicum. Setae siccae valde torquatae et erecto-flexuosae, madidae valde curvatae; capsulae exsertae, oblongo-cylindricae, 1 mm longae, 16-plicatae, magne annulatae, operculo subulato, dentibus peristomii 16, albidis, grosse papillois. Sporae 8–10 μ m, sublaeves. Calyptrae mitratae, lobis 5, patentibus.

Plants small and slender, in dense, dull, yellow tufts. Stems 2–5 mm high, erect-flexuose, simple or forked by repeated innovations, radiculose only at base. Leaves erect to $\pm$ spreading when moist, erect-flexuose when dry, about 1.5 mm



FIGS. 13–20. *Brachydontium curvisetum*. 13. Plant, $\times 15$. 14. Leaves, $\times 32$. 15. Cells at leaf shoulders, $\times 300$. 16. Dry sporophytes, $\times 35$. 17. Calyptra, $\times 35$. 18. Moist sporophyte, $\times 35$. 19. Portion of annulus, $\times 300$. 20. Portion of peristome, $\times 300$.

long below, progressively longer and more crowded upward, as much as 3 mm long, long-subulate from an oblong-ovate base, the subula terete, smooth; margins plane and entire; costa narrow, completely filling the subula; cells of the lamina smooth, moderately thick-walled, irregularly rhombic to subquadrate toward the shoulders, larger and oblong below, not differentiated in the alar regions. Dioicous; male plants mingled with the female, similar but shorter (about 2, sometimes 3 mm high), simple or forked (as many as 3 successive perigonia were seen); perichaetial leaves similar to upper stem leaves. Setae 2–3 mm long, strongly twisted and erect-flexuose to $\pm$ cygneous when dry, strongly cygneous-curved when moist, yellow, smooth; capsules shortly exserted, 1 mm long, oblong-cylindric, without a neck, evenly 16-plicate moist or dry, yellow-brown or tan; annulus broad, revoluble; operculum erect, slenderly long-rostrate from a convex base, about 0.7 mm long; exothecial cells moderately firm-walled, irregularly elongate-hexagonal, somewhat darker yellow in bands corresponding to the ribs, those in 1–2 suboral rows smaller and irregularly hexagonal; stomata very few, small, at junction of urn and seta; peristome teeth inserted near the mouth, erect when moist, recurved when dry, 16, lanceolate, tapered to a narrow apex, consisting of 2 layers of thickenings, white, coarsely papillose, about 125 μ m high, distinctly exceeding the annulus, with a pale, smooth, delicate irregularly dissected low membrane, up to about 35 μ m high, external to the base of the teeth. Spores subspherical, 8–10 μ m, smooth or nearly so. Calyptrae mitrate, about 1 mm long, longer than the operculum but with 5 abruptly spreading lobes near the junction of urn and operculum, smooth, naked.

TYPE: MEXICO. Oaxaca: along road N of Llano de las Flores, N of Oaxaca, on rock, 2000–2500 m, 25 Dec 1965, Z. Iwatsuki & A. J. Sharp 5340 (holotype: TENN; isotype: MICH).

In both gametophytic and sporophytic characteristics, this species is similar to *Brachydontium trichodes* (Web.) Milde, which is rare and scattered at temperate latitudes. It is larger in all its dimensions. More significantly, and more tangibly, it differs in having dioicous inflorescences, cygneous setae, and tapered peristome teeth that clearly exceed the broad annulus. Presumably the low membrane external to the peristome teeth represents the exostome. Although generally placed near the Dicranaceae and the Ditrichaceae, *Brachydontium* and other members of the Seligeriaceae seem to belong to a double-peristome relationship. Only recently has the family been shifted to a separate order, just as the Encalyptaceae, for similar reasons, have been given ordinal recognition.

The generic definition of *Brachydontium* needs to be expanded in order to accomodate the dioicous sexuality and strongly curved setae of this Mexican species.

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A NEW SECTION AND SPECIES OF SPHAGNUM FROM ECUADOR

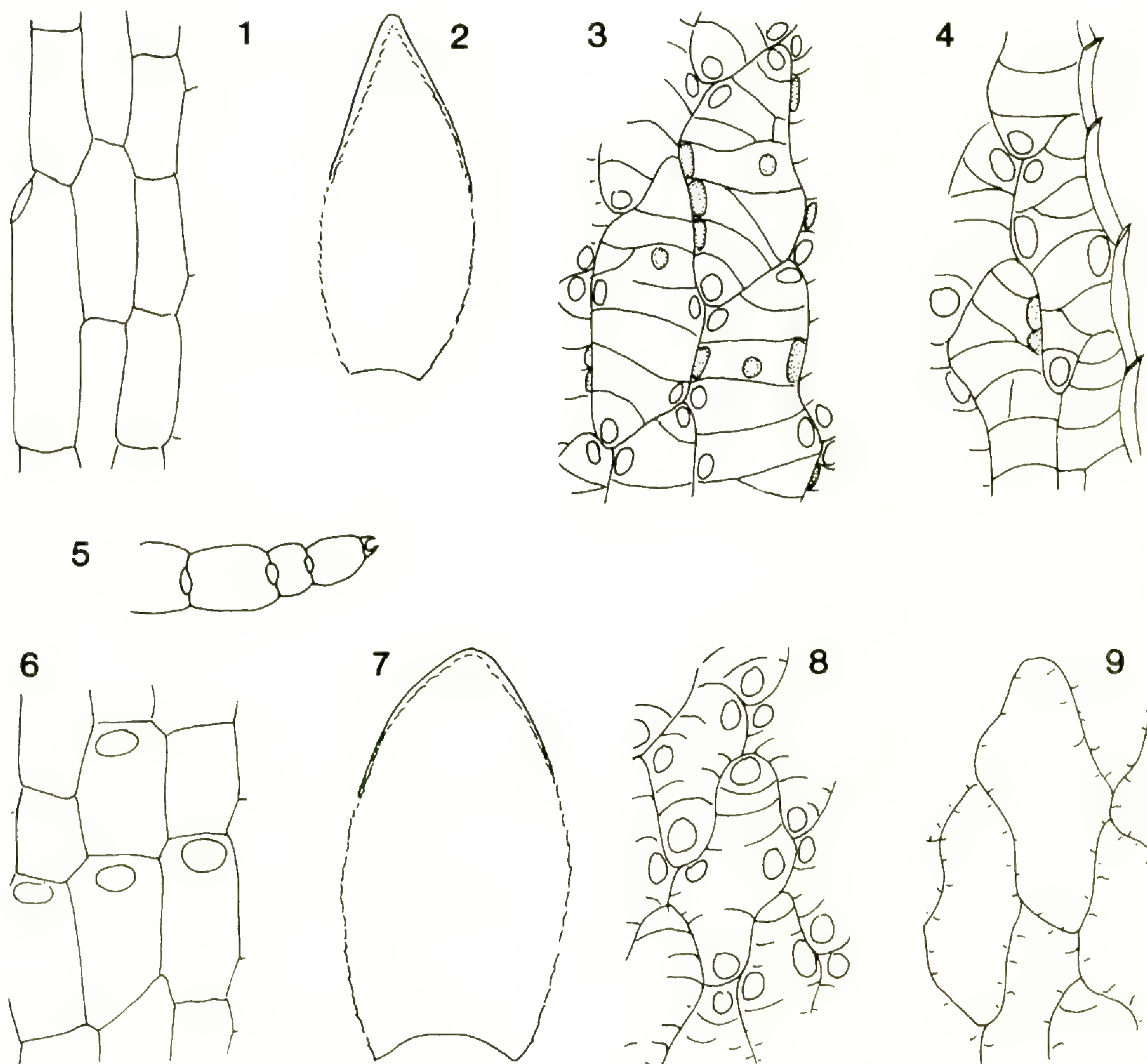
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In the genus *Sphagnum*, resorption furrows are highly distinctive features of the section *Sphagnum* and the section *Rigida*, limited, however, to the branch leaves. I recently received, from William C. Steere, a pretty little *Sphagnum* of Ecuador with resorption furrows at the margins of both branch and stem leaves. The plant shows a number of unique characters that separate it from the sections *Sphagnum* and *Rigida*. The curious occurrence of resorption furrows on the stem leaves seems to justify the erection of a new section of the genus.

***Sphagnum* sect. *Cuculliformes* Crum, sect. nov. et *S. cuculliforme* Crum, sp. nov.¹**

Plants slender, about 5 cm high, pale, brownish white below, pink or pinkish brown above. Terminal bud stout. Stems brown; wood cylinder dark red-brown; cortical cells in 2 (–3) layers, subquadrate to short-rectangular, without fibrils, mostly with a single, large, round pore at the upper end. Stem leaves crowded, loosely erect, shiny brown, relatively large, 1.5–1.7 mm long, concave, broadly elliptic or oblong-ovate, cucullate-obtuse, denticulate-bordered all around because of a marginal resorption furrow; hyaline cells undivided, on the outer surface with fibrils variously reduced, mostly to mere stumps, with 3–4 small, round, ringed pores at the ends and corners, generally grouped in 3's at adjacent angles, in the lower half of the leaf with larger, round, thin-margined pores and also with membrane pleats near the leaf insertion, on the inner surface with fibrils reduced to mere stumps, the membrane nearly all resorbed except near the leaf insertion where there are 2–3 large, round, thin-margined pores about as wide as the cells. Branches in fascicles of 2, similar, both ascending. Branch cortex in 1 layer, consisting of 2 kinds of cells, the retort cells larger, often 1 above another, very short-necked. Branch leaves loosely erect or erect-spreading, concave, 1.1–1.3 mm long, oblong-ovate, obtuse-cucullate, denticulate-bordered all around because of a marginal resorption furrow; hyaline cells fibrillose in the upper half or more, on the outer surface with 2–5 rather small, elliptic, ringed pores at ends

¹Plantae graciles, pallido-fuscae vel subroseae. Epidermis caulium stratis 2–3, efibrosa; parietes exteriores cellularum superficialium foramine uno instructi. Cylindrus lignosus obscure rufo-fuscus. Folia caulina fusca, mediocriter magna, 1.5–1.7 mm longa, late oblongo-ovata, concava, apice cucullato, marginibus lateralibus sulco resorptorio; cellulae hyalinae exteriore superficie ± fibrosae, superne 3–4 poris parvis rotundis in angulis, interiore fere efibrosae, lacunis membranaceis instructae. Fasciculi ramorum e ramulis duobus compositi, cellulis corticis lageniformibus apice pertuso leniter prominulis. Folia ramulina parva, 1.1–1.3 mm longa, oblongo-ovata, concava, apice cucullato, marginibus lateralibus sulco resorptorio; cellulae hyalinae superficie interiore folii poris rotundis magnis prope margines laterales, dorso poris veris ternis in cellularum angulis conjunctis sitis, etiam pseudoporis ad commissuras dispositis; cellulae chlorophylliferae sectione transversali ellipticae, inter hyalinas perfecte mediae, utroque latere foliorum inclusae.



Sphagnum cuculliforme. 1. Branch cortex, $\times 200$. 2. Branch leaf, $\times 30$. 3. Upper cells of branch leaf, outer surface, $\times 300$. 4. Upper marginal cells of branch leaf, outer surface, showing resorption furrow, $\times 300$. 5. Portion of branch leaf in section, $\times 200$. 6. Stem cortex, $\times 200$. 7. Stem leaf, $\times 30$. 8. Upper cells of stem leaf, outer surface, $\times 300$. 9. Upper cells of stem leaf, inner surface, $\times 300$.

and corners, generally in 3's at adjacent angles, also frequently with few to several, thin-margined, narrowly elliptic pseudopores at the commissures and, especially toward the leaf apex, often with 2–3 very small, round, unringed pores or pseudopores in a more median position, in the lower half of the leaf with 2–3 large, round, thin-margined pores, on the inner surface with few to several narrowly elliptic, thin-margined pseudopores at the commissures; green cells in cross section elliptic, central, entirely included, the hyaline cells slightly convex on both surfaces, with smooth inner walls. Inflorescences and sporophytes unknown.

TYPE: ECUADOR. Steep rocky slopes with scattered shrubs, 2200–2250 m, General Plaza (Limón)-Gualaceo road, 18–20 km from Limón, 12 June 1979, B. Løjtnant, A. & U. Molau 14627 (holotype: MICH; isotype: NY); paratype: 14611 MICH, NY).

Important characters include outer cells of the stem cortex uniporose and lacking spiral fibrils; stem leaves broadly oblong-ovate, cucullate-concave, bordered by a resorption furrow and having hyaline cells more or less fibrillose, with small pores in 3's at adjacent angles on the outer surface and, on the inner surface, with the wall mostly resorbed so that the fibrils are reduced to mere

stumps; branches in pairs, stout and spreading to ascending; branch cortex consisting of retort cells in addition to non-porose cells; branch leaves somewhat smaller and narrower than stem leaves, cucullate-concave, bordered by a resorption furrow but not roughened at back of the apex; hyaline cells with small pores in 3's at adjacent angles (and also some commissural pseudopores and a scattered few, round, median pores or pseudopores) on the outer surface; green cells central and included.

The species has some resemblances in aspect to *Sphagnum magellanicum* Brid., in the section *Sphagnum*, owing to the pinkish tinges of the upper, exposed leaves and their broad, hooded, and imbricate nature. Also the green cells of the branch leaves are central and entirely included. In the cross-sectional nature of the green cells and the tendency to show numerous pseudopores in the branch leaves, it also resembles *S. compactum* DC., in the section *Rigida*. These are merely incidental similarities, giving no evidence of close relationship. The section *Sphagnum* differs in many ways. It has clearly differentiated stem and branch leaves. The stem leaves are flat, lingulate, and bordered by a fine-meshed fringe. The cells of the stem cortex are most generally fibrillose, and those of the branch cortex are also commonly fibrillose and they are uniform in size, shape, and structure, none of them differentiated as retort cells. The branch leaves are roughened at back of the apex because of resorption. The *Rigida* have very small stem leaves with entire margins, and the branch leaves are truncate and not hooded at the tip. All cells of the branch cortex are porose at their upper ends and retortlike. Furthermore, the pores are grouped in 3's on the inner rather than the outer surface of the branch leaves.

A PRELIMINARY STUDY OF CORALLORHIZA MACULATA (ORCHIDACEAE) IN EASTERN NORTH AMERICA

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INTRODUCTION

Corallorhiza Chat. is a genus of 10 to 15 species of leafless orchids confined largely to North and Central America (only *C. trifida* is found in the Old World). The genus is similar in habit to several other genera of leafless orchids, including the North American *Hexalectris* Raf. and one species of *Cephalanthera* Rich. Close examination of the flowers reveals significant differences in column structure and development between the genera, reflected in their placement in separate subfamilies by Dressler (1981).

Although no monographic work has been done on *Corallorhiza*, at least 50 species have been proposed. One of the most common species, *C. maculata*, was named in 1817 by Rafinesque based on material from coastal New York. Subsequent collecting in the United States and Canada produced specimens from as far west as California and British Columbia, which possessed the spotted lip of *C. maculata* and hence were called by that name (or *C. multiflora* Nutt., which, although a later synonym, was in common use for many years).

Ames may have been the first to discuss the idea of a significant pattern of morphological variation within *C. maculata* when in 1913 he wrote to Cockerell: "I have always been impressed by the fact that eastern and western specimens referred to *C. maculata* are distinguishable in the herbarium, and the difference has been noted by other observers . . . That there is a difference between them, nobody who has made a careful study of the subject will deny, but if a geographical demarcation can be made which will show that the two forms occupy distinct or practically distinct ranges I would favor specific differentiation" (Cockerell 1916).

More recently, several individuals have independently noted a pattern of variation in *C. maculata* in the Great Lakes region (R. Brown, D. Henson, and A. A. Reznicek, pers. comm.). The pattern they observed involves two distinct morphological entities blooming at noticeably different times. These observations suggested that further study of this group was necessary, the first step being a morphological analysis of *C. maculata*.

METHODS

Approximately 800 specimens of *C. maculata* were examined from across North America, exclusive of Mexico. Morphometric data were obtained by measuring characters for one flower at the middle of one raceme per herbarium sheet; 117 specimens were measured to compare floral bract length with lip proportions. Because of the complexity of *Corallorhiza* flowers, it is difficult to press the plants

in a manner which retains the flowers' shape and allows accurate measurement of all characters on the same flower. For example, in many cases a flower on which lip width was measurable had an obscure or missing floral bract. In such instances, the bract was measured on a neighboring flower near the center of the raceme and at the same stage of development.

In addition to study of herbarium material, field work was undertaken in Michigan and Ontario to study habitats and phenology and to make additional morphological observations. Several racemes of flowers were collected and fixed in FAA (Cutler 1978) for later dissection and examination.

MORPHOLOGICAL FINDINGS

Field study of *Corallorhiza maculata* in the Great Lakes area indicated that lip shape, overall flower size, and length of floral bracts were significantly variable characters. The variability is not random but rather follows a pattern: plants with large flowers are found to have broadly dilated lips and long, usually furcate bracts; the smaller-flowered plants have narrow, almost parallel-sided lips and small, entire bracts. Examination of herbarium specimens confirmed this pattern for eastern North America. A "lip index" was used to quantify the dilation of the apical portion of the lip. This index was obtained by dividing the width of the broadest area near the apex by the width between the lateral lobes. Lips with no dilation have an index of 1.0; dilated lips have an index greater than 1.0. A scatter plot of lip index against bract length shows a positive correlation between the characters when collections from across North America are plotted (Fig. 1). Collections from east of 105°W longitude are separated into two fairly distinct groups on the basis of these characters. Some collections from west of 105°W longitude appear to connect the two groups from the east. This suggests intermediacy in these characters for some of the western plants. Examination of additional western specimens confirmed this pattern. Many western specimens could be separated, as in the east, into two groups of dilated lip-long bracted individuals and a very few with nearly parallel-sided lips and short bracts; however, a significant number (ca. 20%) showed intermediate bract length and degree of dilation. In addition, some specimens showed a "mixing" of character states (e.g., plants with long bracts and barely dilated lips).

The two groups of *C. maculata* in the east are distinguished by additional morphological characteristics (Table 1; Fig. 2). Many of these are almost impossible to measure accurately from pressed material; therefore, a statistical analysis of the difference in morphological characteristics between the two groups was not attempted. As can be seen from the table, morphological features tend to be larger in early *C. maculata* than in late *C. maculata*. Most of these characters are self-explanatory; one feature which may not be obvious is the sepal sinus. This structure is formed by the fusion of the lateral sepals on the ovary on the distal side of the mentum (Fig. 2c, f).

Certain other qualitative morphological differences serve to differentiate the groups. The angle of carriage of individual flowers tends to be greater (more upward) in early *C. maculata* than in late *C. maculata*, although this is quite variable and dependent upon stage of development. Flowers of early *C. maculata* frequently have larger menta than those of late *C. maculata* at a comparable stage of development. Early *C. maculata* flowers frequently appear more open or somewhat flatter than do flowers of late *C. maculata* (which tend to have somewhat

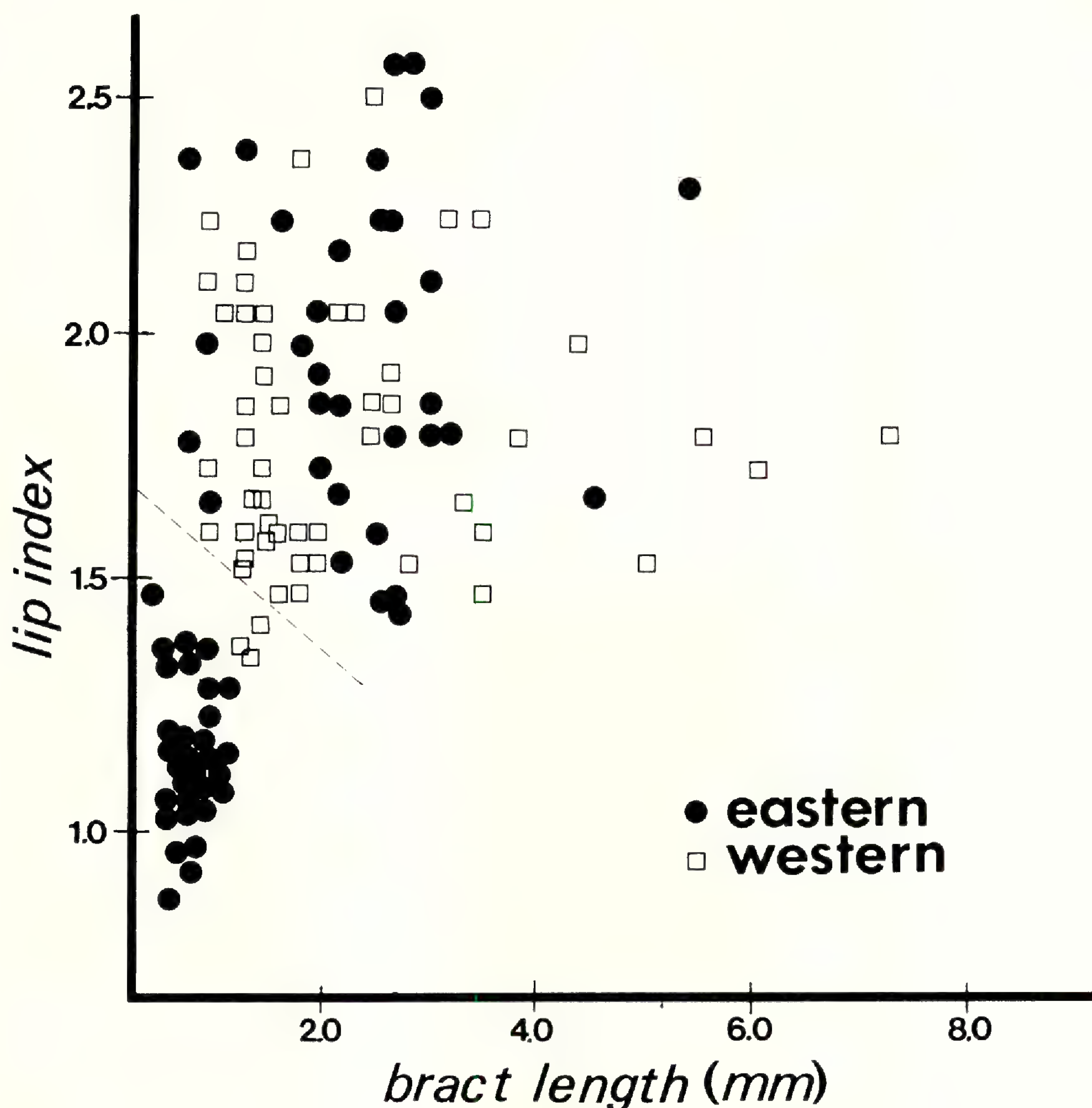


FIG. 1. Scatter plot of lip index versus floral bract length of 117 specimens of *Corallorhiza maculata*. The dashed line indicates the groups of eastern specimens.

involute lip apices). Inflorescences of early *C. maculata* tend to be clumped rather than single as in most late *C. maculata*. Although many western specimens show the character combinations described here, a significant proportion display intermediacy for these features as they do for lip proportions and bract length. The analysis of these patterns requires extensive field study in the western portion of the range of *C. maculata* and is beyond the scope of the present preliminary study; however, the distinct combinations of these morphological characteristics make the two groups easily recognizable in the eastern half of North America (Figs. 3, 4).

PHENOLOGICAL AND ECOLOGICAL OBSERVATIONS

The morphological variation shows a correlation with bloom time for the two groups of *C. maculata*. Field study and data from dried specimens indicate that

Table 1. Characteristics of early and late *Corallorhiza maculata*.

	Early	Late
Lip dilation (lip index)	>1.3	<1.3
Floral bract length	>1.0 mm	<1.0 mm
Column length	(3.1) 3.8–5.6 mm	3.0–4.6 mm
Pedicellate ovary length	8.6–13.0 mm	7.2–9.4 mm
Number of flowers	18–40	10–20
Sepal sinus shape	broad, shallow	narrow, deep

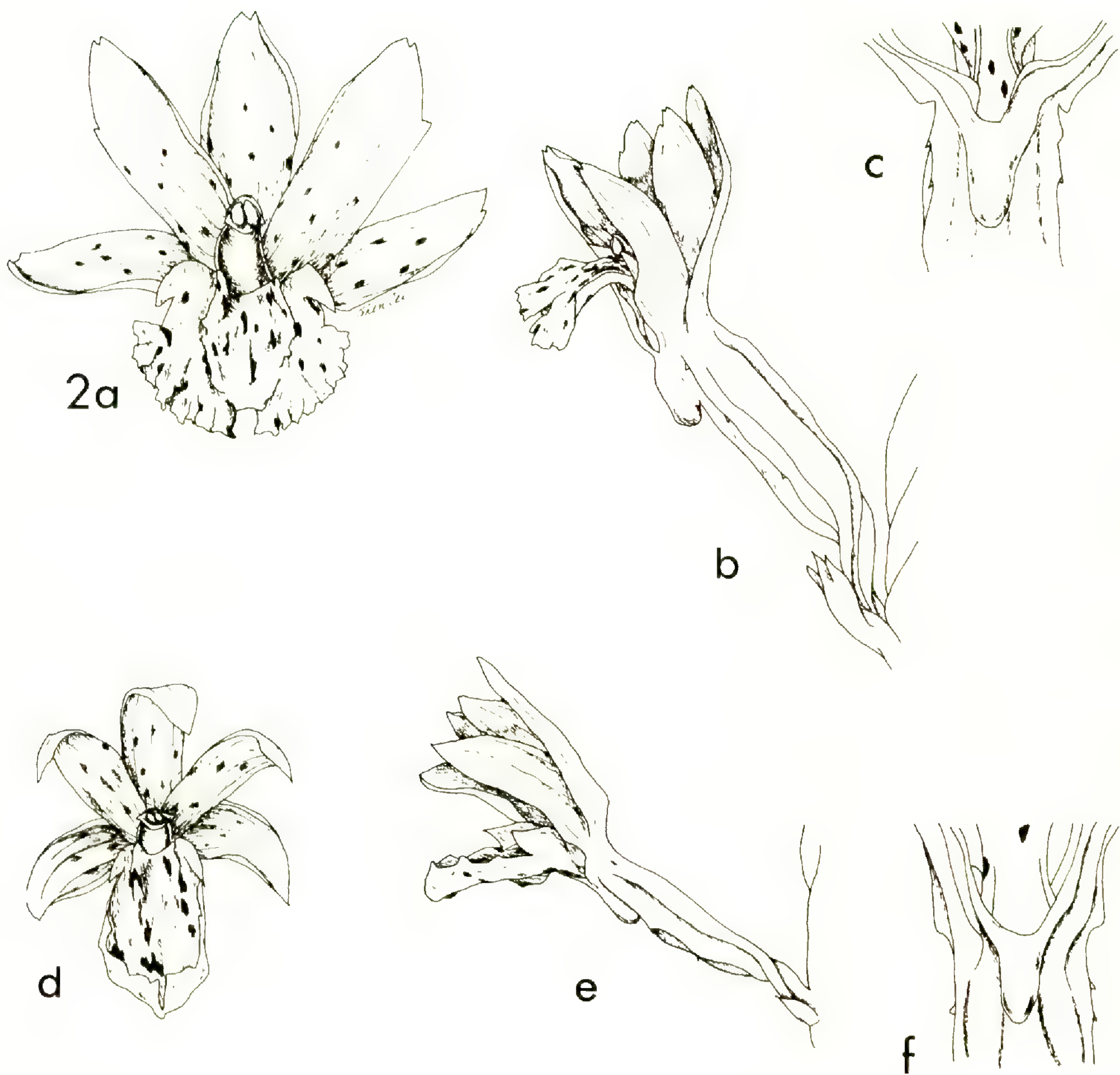


FIG. 2. Flowers of *Corallorhiza maculata*. a–c, early *C. maculata* flower. a. Front view, $\times 4$. b. Side view, $\times 3$. c. Seen from below, $\times 6$. d–f, late *C. maculata* flower. d. Front view, $\times 2.5$. e. Side view, $\times 3$. f. Seen from below, $\times 7$.

early *C. maculata* is at peak bloom approximately 2–4 weeks before late *C. maculata* at the same latitude and in comparable habitats. Table 2 shows eight specimens of *C. maculata* from central New York and their dates of collection. It is difficult to compare such collections because of yearly and seasonal differences as well as microhabitat variation; nevertheless, a striking difference can be seen between the two morphological groups. Since the length of flowering for a par-



FIGS. 3–4. Inflorescences of *Corallorhiza maculata*. 3. Early *C. maculata* (Schoolcraft Co., Michigan, June 1983). 4. Late *C. maculata* (Cheboygan Co., Michigan, July 1984).

ticular raceme may be ca. 2 weeks, total temporal isolation between the groups may not be achieved; however, gene flow between the groups is probably restricted to a significant degree. Occasionally, both types of *C. maculata* will be found growing together, allowing an opportunity for comparison. This situation occurs on Isle Royale National Park in northern Michigan. There, plants with the features described for early *C. maculata* were found to be at peak anthesis on July 9, 1985. Approximately 6 m away, other specimens of *C. maculata* were found still in tight bud. Careful dissection of buds showed that the plants had the morphological characters of late *C. maculata*. Other closely sympatric occurrences are known for the groups, and several mixed collections have been found on herbarium sheets from across North America.

Although the two groups of *C. maculata* can be found in the same habitat toward the northern limits of their distributions, in more southern localities there are distinct habitat preferences for each group. Hence, in areas where northern

Table 2. Flowering dates for early and late *Corallorhiza maculata* from central New York.

Early <i>C. maculata</i>	
Cayuga Co., Summerhill, <i>Atwood s.n.</i> (CU), 18 June 1878.	
Schuyler Co., Hector, <i>Eames s.n.</i> (CU), 16 June 1918.	
Tompkins Co., McLean, <i>Kilborne s.n.</i> (CU), 25 June 1879.	
Tompkins Co., near Dryden Lake, collector unknown, (CU), 25 June 1875.	
Late <i>C. maculata</i>	
Schuyler Co., Catherine, <i>Gershoy s.n.</i> (CU), 2 Aug 1918.	
Tioga Co., Owego, <i>Mapes s.n.</i> (CU), 12 July 1914.	
Tompkins Co., Dryden, <i>Eames et al. s.n.</i> (CU), 20 July 1919.	
Tompkins Co., Newfield, <i>Wiegand, s.n.</i> (CU), 30 July 1916.	

coniferous or mixed forests predominate (including species of *Pinus*, *Picea*, *Betula*, *Acer*, *Ostrya*), both early and late *C. maculata* may be found together in this habitat. However, where both rich deciduous forest and conifer woods are present in more southern locations, early *C. maculata* will be found almost exclusively in the coniferous areas (especially along cool lake shores), whereas late *C. maculata* will be found predominantly in the deciduous forest. Late *C. maculata* seems to have a somewhat broader habitat tolerance than does early *C. maculata* (e.g., late *C. maculata* was occasionally found in cool coniferous woods in more southern areas; early *C. maculata* was never found in rich deciduous woods). These habitat differences may in part determine the range of each of the groups. Early *C. maculata* tends to be more northern (Fig. 5), although there is a great deal of overlap with the somewhat more southern late *C. maculata* (Fig. 6).

DISCUSSION

It is clear that in the eastern portion of North America what has been considered a single taxon, *C. maculata*, is actually two groups of plants distinct on the basis of morphology, phenology, and to some extent habitat. Morphological differences could reflect adaptation to different pollinators, if indeed the plants are outcrossing. Habitat differences could be due in part to ecological requirements of the fungal associates (which may be species-specific) known to form endomycorrhizal relationships with *Corallorhiza* (Campbell 1970). The significance of these groups cannot be fully understood until the pattern of variation in the western populations has been studied. It is possible that early and late *C. maculata* are distinct species that have undergone hybridization in western North America but not in the East. This difference might be accounted for by the difference in topography between the East and West. Western mountainous areas provide a great variety of microhabitat conditions (due to altitude changes, different exposures, etc.) in a relatively small area of land. The variety of microhabitats may support both early and late *C. maculata* in close proximity to one another. It is possible that these habitat differences could cause a particularly large overlap in flowering periods of the two groups (an early blooming plant in a particularly cold location might bloom at the same time as a late blooming plant in a warm site). The frequent opportunity for hybridization thus produced in the West would not be expected in eastern North America, which has a much less variable topography over most of the range of *C. maculata*.

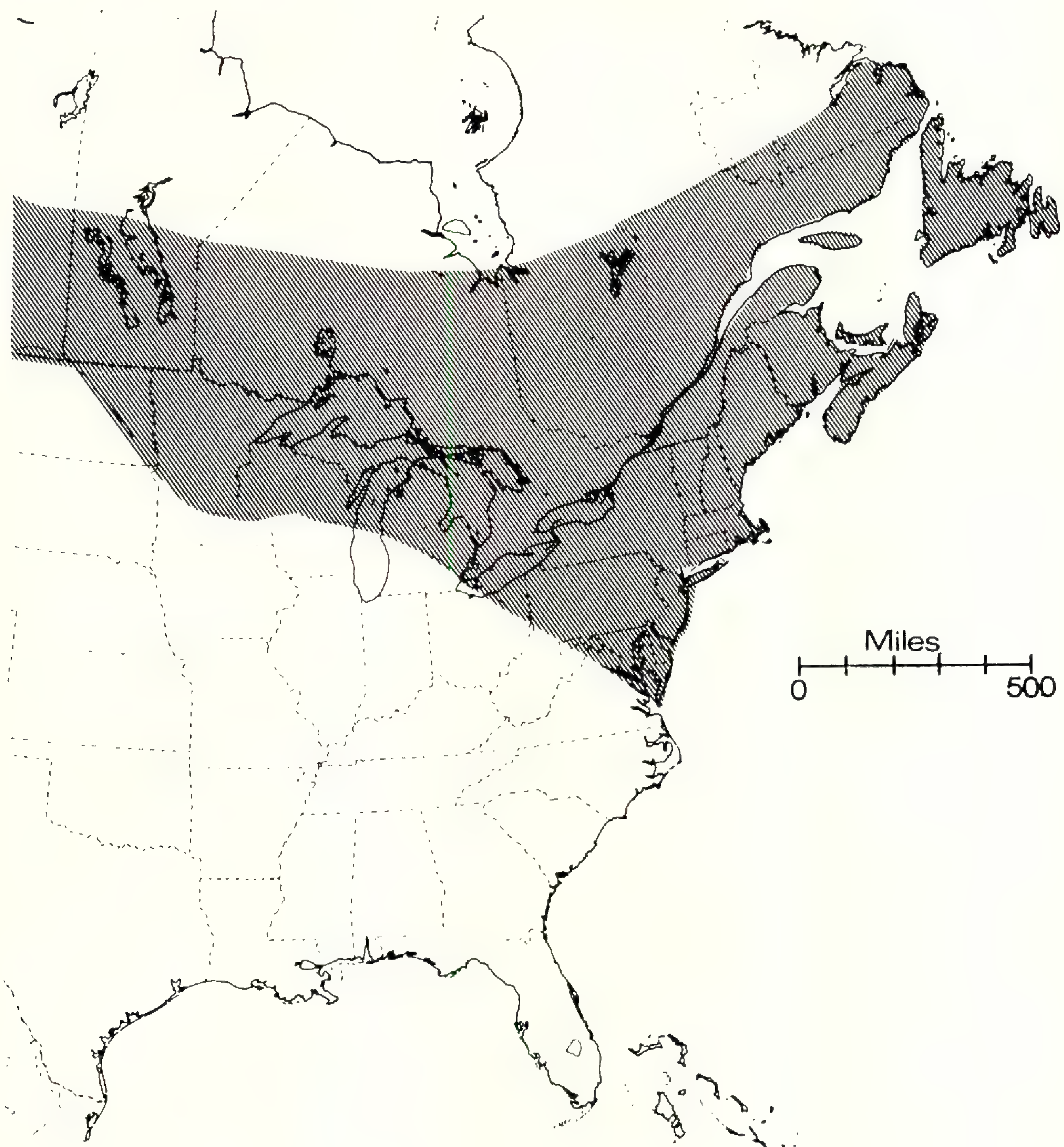


FIG. 5. Distribution of early *Corallorhiza maculata* in eastern North America.

Also, *C. maculata* varies greatly in color. It appears that two at least partially independent color factors operate to produce the combinations seen in the plants. Bartlett (1922) suggested that anthocyanins and other flavonoids combine in various proportions in *C. maculata*. The range of coloration includes dark purples, reds, browns, and pure yellow. Several of these variants have been named as forms and varieties of *C. maculata*. The coloration does not preserve well in pressed plants, which makes analysis from herbarium specimens very difficult. However, forma *flavida* (Peck) Farwell is so distinctive that it can usually be detected in dried specimens. In this form the lip is white, unspotted, and the rest of the plant is pure yellow (presumably deficient in anthocyanins). During this study it was found that all specimens of f. *flavida* (from scattered localities across North America) were referable to early *C. maculata*. Case (1964) suggested that this coloration may be particularly attractive to pollinators and therefore may be

Henson 1061 (MICH). Montana: Echo Lake, *Kaufman & Cummins 140* (MICH); Flathead Co., *Hitchcock 24504* (WTU); Lake Co., *Hitchcock 17725* (WTU). New Mexico: Rio Arriba Co., *Hershey 3881* (AMES). Oregon: Josephine Co., *Ownbey 3317* (WTU). South Dakota: Sylvan Lake, *Johnson s.n.* (MICH). Utah: Garfield Co., Henry Mts, *McVaugh 14645* (MICH). Washington: Skagit Co., *McElvain 135* (WTU). Wisconsin: Vilas Co., *Richards 3498* (MICH). Wyoming: Albany Co., *Kaufman & Erlanson 22* (MICH); Albany Co., *Porter 7034* (WTU).—CANADA. Manitoba: E of Winnipeg, *Scoggan 8772* (AMES). Ontario: Algoma Dist., Goulais R., *Freudenstein 768* (MICH); Manitoulin Is., West Bay, *Grassl 2380* (MICH); Thunder Bay Dist., *Garton 2881* (LKHD), *19519* (MICH). Saskatchewan: Nipawin Prov. Park, *Argus 4114* (AMES).

Late *C. maculata*: U.S.A. Connecticut: Salisbury, *Nichols*, July 1905 (MICH). Indiana: Porter Co., *Cusick & Furlow 23719* (MICH). Maine: Franklin Co., *Herb. Eaton*, 15 Jul 1903 (AMES); Penobscot Co., *Williams*, 17 Jul 1900. (AMES). Massachusetts: Norwood, *Kennedy 1* (AMES); Hyde Park, *Herb. Faxon*, 7 Aug 1890 (AMES). Michigan: Chippewa Co., Drummond Is., *McVaugh et al. 11357* (AMES, LKHD, MICH); Grand Traverse Co., *Dieterle 1334* (MICH); Montcalm Co., *Case & Case*, 25 Aug 1965 (MICH); Muskegon Co., Cedar Creek Twp, *Voss 3242* (MICH); Oakland Co., Addison Twp, *Billington*, 29 Jul 1928. New York: Buffalo, *Clinton s.n.* (MICH); Lake George Region, *Burnham 9* (WTU). Ohio: [Champaign Co.], *Samples*, 26 Aug 1937 (MICH). Pennsylvania: Parkside, *Beuchseatt*, 30 Aug 1927 (MICH); Warren Co., *Moldenke 15589* (AMES). Vermont: Ascutney Mt., *Taylor*, 20 Sep 1915 (MICH); Fairlee, *Denslow*, 27 Jun 1912 (AMES). Virginia: Botetourt Co., *Freer et al. 7184* (ASU). Wisconsin: Bayfield Co., *Voss 10035* (MICH).—CANADA. Nova Scotia: Annapolis Co., *Bartram & Long 23733* (AMES). Cape Breton Is., Tarbet Vale, *Nichols*, 3 Aug 1915 (MICH). Ontario: Thunder Bay Dist., Burchell Lake, *Garton 20320* (LKHD, MICH); *Pease & Bean*, 6 Jul 1933 (AMES); Sibley Prov. Park, *Voss 10209* (MICH). Québec: Meach Lake, *Malte*, 17 July 1923 (MICH).

Specimens intermediate between early and late *C. maculata*: U.S.A. California: Del Norte Co., *Denton 2857* (WTU); San Diego Co., *Abrams 3863* (AMES). Colorado: Tabeguache Basin, *Payson 128* (WTU). Idaho: Blaine Co., *Macbride & Payson 2947* (RM); Caribou Co., *Wetherell 349* (RM). Montana: Lake Co., *Hitchcock 17725* (RM); Missoula Co., *Cronquist 7883* (AMES). Nevada: Baker Creek, *Gray 191* (RM). Oregon: Josephine Co., *Kruckeberg 1983* (WTU); SE of Port Oxford, *Peck 8644* (AMES). Washington: Mason Co., *Freer 399* (WTU). Wyoming: Carbon Co., *Mastrella 45* (RM).—CANADA. British Columbia: *Rosendahl 1903* (AMES).

ACKNOWLEDGMENTS

This paper is part of a Senior Honors Thesis project undertaken at the University of Michigan. I thank A. A. Reznicek for bringing this project to my attention and for his constant help and suggestions as well as for supplying me with some preserved materials. I am grateful to E. G. Voss, my thesis advisor, for his critical reading of the thesis and suggestions, and to W. H. Wagner, Jr., for reading the paper and for ideas which grew out of discussions with him. I also thank J. J. Doyle for his comments on this manuscript. I am indebted to F. W. and R. B. Case, D. Henson, A. A. Reznicek, and T. A. Freudenstein, who assisted in the field work and showed me localities. G. F. Estabrook's assistance in using the computer is appreciated.

I acknowledge the curators of the following herbaria for loans and for their courtesies during my visits: AMES, BH, BLH, CU, GH, LKHD, MICH, MSC, PH, RM, and WTU. Field work was supported by a grant from the University of Michigan Honors Council's Cutcheon Fund and by grants from the Hanes Fund. The illustrations were drawn by Shenlei Winkler. I thank Bente S. K. Everhart for help in preparing the figures. Use of computer time was made possible by funds from the Division of Biological Sciences, University of Michigan.

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BOTANICAL RESULTS OF THE SESSÉ & MOCIÑO EXPEDITION (1787–1803)

III. The Impact of this and other Expeditions on contemporary Botany in Europe

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Still mostly unwritten is the story of the American plants that were collected by the *Expedición Real de Botánica* (the “Sessé & Mociño expedition”) and other Spanish expeditions of the period, subsequently grown in the Royal Botanical Garden at Madrid, and thence distributed widely to the principal gardens of Europe. Several hundred new species of flowering plants were described by Spanish botanists between 1791 and 1816 in special publications. The contribution to horticulture, through the introduction and dissemination of such genera as *Cosmos*, *Dahlia*, *Tagetes*, and many others, was relatively enormous. The circumstances under which botanical publications resulted were unusual, and in order to evaluate the contribution made to botany and horticulture by the Sessé & Mociño expedition it is necessary to fill in some of the background of the expedition, and also to include some mention of other Spanish expeditions of the period, specifically the Malaspina expedition (1789–1794)¹.

First it may be noted parenthetically that the 18th-century expeditions were unlike modern plant-explorations. The 18th-century explorers did not expect to return quickly to centers of learning where they could study their plants at leisure and publish conveniently. The members of the Royal Botanical Expedition lived in Mexico City, some of them for more than a decade. Some of them married, and some died. The botanists of the expedition had a good library (brought from Spain), which they used to name and describe the plants they found, but they did not expect to publish their findings until they returned to Spain, as they ultimately did in 1803. In the meantime they continued to send back, as opportunity offered, such plants as seemed appropriate for cultivation in Spain. It was from these contributions that the Spanish botanists soon began to grow new and interesting plants.

The most important and influential botanist in Spain at the time of the organization of the *Expedición Real de Botánica* was Casimiro Gómez Ortega (1740–1818), an account of whose life was given by Colmeiro (1858). (Colmeiro, in accordance with hispanic usage, calls him Gómez Ortega, but his contemporaries, including Cavanilles, called him Ortega, and in documents I have seen he signed his name Casimiro Ortega, so in this paper he appears as Ortega). Ortega studied botany and medicine in Italy. In 1771 he was placed in charge of the Royal Botanical Garden in Madrid, a post he held for the next 30 years. During his

¹For previously published contributions to knowledge of the botanical results of the Sessé & Mociño expedition, see McVaugh (1977, 1980).

directorship the Garden was moved in 1781 to the central location it still occupies, on the Prado a short distance from the center of Madrid (Steele 1964, pp. 37–39). He was generally responsible from the beginning for planning Spanish participation in the expedition to Peru (1777–1788), and it was he who had the last say in the appointment of Ruiz and Pavón as the botanists to that expedition.

It was Ortega to whom Sessé wrote in 1785 to urge the organization of an expedition to Mexico, and the establishment of a botanical garden and a chair of botany at the University there. To Ortega belongs much of the credit for the initial success of the venture and, after Royal approval had been secured in 1786, the expedition was organized, staffed, and fitted out with his aid (Wilson 1962, pp. 3–9; Engstrand 1981, p. 13). Longinos Martínez and Cervantes had been his pupils, and his relations with Sessé were cordial. Because of his position as first professor at Madrid, most of the materials intended for the Royal Botanical Garden presumably passed through his hands. Soon after the formal establishment of the expedition in Mexico, in August, 1787, the first consignments of seeds and living plants began to reach Madrid, and a trickle of such contributions, usually transmitted officially through the Viceroy, continued until 1803.

There are a number of records, published and unpublished, of specific items transmitted to Madrid from Mexico (cf. Alvarez López 1952; Arias Divito 1968; Wilson 1962; Engstrand 1981; Rickett 1947). The shipments began after the first explorations near Mexico City in 1788. Living roots of *Jalapa* were to be sent in 1789. In November of the same year, seeds of more than 75 species were forwarded after the expedition returned from the “Second Excursion” (cf. McVaugh 1977), that to Guerrero.

Additional records of similar activities are in the archives of the Instituto Botánico “A.J. Cavanilles” (MA). As a result of the “Third Excursion”, that to western Mexico in 1790–91, seeds of 58 species were sent to Spain in December 1790, and of 41 additional species in March 1791. Seventy species were sent in November 1791. In March 1793 Sessé consigned 10 boxes of living plants for the Royal Garden (about 40 species, mostly succulents including 6 species of *Sedum* and 13 cacti), to the care of Don Cristóbal Quintana who was returning to Spain.

In addition to seeds and living plants collected in the field by Sessé and the others, some plant material was apparently forwarded by Cervantes from the Botanical Garden in México. Doubtless a part of this material consisted of seeds of wild plants from near México, and a part of cultivated plants. The garden in México, from about 1790 to 1803, was active but not very large. Cavanilles (Anal. Ci. Nat. [Madrid] 6 (no. 18): 281–287. [?Oct.] 1803) published excerpts from a letter by Humboldt, written from México on April 22, 1803, and appended to this a note from Bonpland, who had visited Cervantes in the Botanical Garden, and thought moderately well of both: “El jardin de México no es muy grande, pero está bien cuidado, y dispuesto con el acierto propio del Señor Cervantes. Este profesor tiene mucha instrucción y mérito, que es justo se conoce en Europa”. The Garden in Madrid, in 1803, received material of 100 species from Cervantes (Cavanilles, op. cit. 330). Cervantes remained in Mexico after his associates returned to Spain. He survived the Revolution and, as will be noted later, was sending plant materials to Europe almost to the time of his death in 1829. Arias (1968, p. 40) says that as late as 1815, in the midst of the Revolution, Cervantes forwarded to Madrid a shipment of seeds of 281 species of Mexican plants.

Here then are records of 500–600 species of Mexican plants sent for trial in a European garden by members of the botanical expedition. Doubtless there

were more of which no record has been found. It was by any standard a sizeable contribution. It would be very interesting to know just which ones survived and which did not. Perhaps somewhere in the archives at Madrid there are files of old cultivation records dating back to the 18th century, but I have not seen them and have to rely on other accounts. We know that many of the introductions prospered.

When the botanist Cavanilles returned to Madrid in the autumn of 1789, after an absence of two years in France, he wrote on November 23rd to A. L. de Jussieu, describing the pleasure he had experienced on going to the Madrid Garden and finding there in bloom a number of extraordinary plants from Mexico and Peru. Subsequently, in the preface to the first volume of his *Icones*, under date of the Kalends of January, 1791, Cavanilles acknowledged with more than ordinary politeness the contribution that had been received from Mexico: "In Nova Hispania Vicentius Cervantes et Iosephus Longinos una cum Iosepho Antonio Alzate plantarum indagini continenter vacant, rariorumque semina mittunt ad nos; ut adeo ipsorum diligentiae debeantur plantae praestantiores, quibus Hortus Regius Matritensis ornatur."

Ortega lived to see the *Expedición Botánica* return from New Spain, but his powers and his influence had declined before the end of the century, and in 1801 he was supplanted as director and first professor by the more aggressive, active, and vocal Antonio José Cavanilles (1745–1804).

Cavanilles was a native of Valencia, where he studied Philosophy and Theology at the University, preparing himself for an ecclesiastical career. He taught Philosophy for a time, then became the tutor of the Duke of the Infantado. In the course of these duties he made a trip to Paris in 1777. In Paris, from 1781 onward, he devoted himself to the study of the Natural Sciences, especially to Botany, to which he became attracted especially through the lectures of A. L. de Jussieu (Colmeiro 1858, p. 173). He made his first botanical reputation with his *Monadelphiae classis dissertationes decem* (1785–1790). He returned to Spain for a time in 1787, and in 1789 settled permanently in Madrid. He soon became embroiled in one controversy after another, especially with Ortega.

According to Cavanilles' own published account of his *Controversias* (Cavanilles 1796, pp. 20–21, etc.), Ortega had praised the early work on the *Monadelphiae* both publicly and privately, and had encouraged Cavanilles to continue for the glory of Science and for that of Spain. When Cavanilles returned to Spain in 1787, however, and especially when it became evident that he would remain, Ortega turned against him. Steele (1964) surmised that the original differences may have been caused by Ortega's fear that Cavanilles had been brought in to replace him at once as head of the Botanical Garden. Whatever the truth may have been, relations between the two men worsened steadily until the time of Ortega's retirement. After the early 1790s they seem not to have been on speaking terms, though both were studying, quite independently, and publishing upon, the plants received from New Spain and grown at the Royal Botanical Garden (an account of this series of personal vendettas, with much background information, is provided by Steele, especially pp. 240–245).

Exchanges between Ortega and Cavanilles took the form of published criticism of each other's work. Ortega seems to have been the gentler (or more restrained) soul, who rarely wrote direct criticism of others, but Cavanilles was outspoken (at his mildest) to insulting, in his letters and in his published writings. Indeed such conflict seems to have been a part of his character. The vigor with

which he pursued his controversies seems to have been matched by the vigor with which he did other things. Soon after his establishment in Madrid (Steele 1964, p. 242), he was given an order to examine the plants of the Royal Garden, and publish an account of them. He is quoted as saying that this came about because Ortega had been Professor at the Garden for 18 years and had done nothing about preparing such an account. In any event, as a result of Cavanilles' labors, there appeared in print in a remarkably short time (on February 16, 1791) the first part of what was eventually to be a 6-volume set, *Icones et descriptiones plantarum*, in which 600 species mostly new to Science were described and illustrated.

This was the first important post-Linnaean work that was devoted to any great extent to Mexican botany. Linnaeus, Miller, Lamarck and others had described in passing a few Mexican species, but these mostly incidentally to their main purposes. Cavanilles, on the other hand, devoted about one-third of his *Icones* to new and original descriptions, and illustrations, of plants grown at the Royal Botanical Garden from Mexican seeds. He described in all about 200 Mexican species, of which about 185 were new, or thought to be new, to Science. About 135 of the new species were described from garden-grown plants, and the rest were based on specimens from the herbarium of Luis Née, one of the botanists of the Malaspina expedition, whose collections became available to Cavanilles in 1794 or soon thereafter.

In the first two volumes of the *Icones* (publ. 1791 to ca Jan 1794), and in the first part of the third volume (April 1795), the new Mexican species described from garden-grown plants probably all came from seeds sent by Cervantes and Sessé or their associates, though Cavanilles never acknowledged this for any specific item. Cavanilles seems never to have mentioned Sessé, though he must have been aware of the latter's involvement in the work in New Spain. I can only surmise that this was because of the continuing friendship between Sessé and Ortega. Cavanilles' early (January 1791) acknowledgment to Cervantes and Longinos, quoted above, may have been made before the controversy with Ortega had become fever-hot.

The 30 new Mexican species described in the first volume of the *Icones* were all published in 1791; when dates of flowering are given, the years range from 1788 to [March] 1791. The last plate (no. 100, *Verbesina pinnatifida*) was completed and sent to A. L. de Jussieu for comment, by 12 February 1791. The species in this volume, beyond any reasonable doubt, represent the first published contribution from the Royal Botanical Expedition to New Spain. The Malaspina expedition contributed little or nothing to the early volumes of the *Icones*. The surviving part of that expedition did not return to Spain until 21 September 1794 (Wilson 1962, p. 106; Engstrand 1981, p. 106), so any seeds or other propagules reaching Madrid before that must have been forwarded in advance. A large shipment of manuscripts and natural history materials was prepared by the scientists of the expedition as the ships were leaving Acapulco at the end of December, 1791. This was consigned to the Viceroy, Revilla Gigedo, for transmittal to the Crown (Wilson 1962, pp. 178–181; Engstrand 1981, p. 103). If seeds or living plants were included they may have reached Madrid by the middle of 1792, but hardly much before that.

In the first part of the third volume of the *Icones* (Cav. Ic. 3: 29. Apr 1795), in the account of *Ipomoea pentaphylla*, the plant was said to have flowered in Madrid in August, 1794, "ex seminibus missis ab Hispanis qui orbem circum-eunt". This seems to be the earliest mention of the plants that were received from

the Malaspina expedition, the "Spaniards that went around the world." Except for this example, I do not find any clear implication that seeds or other plant-parts were sent ("*missis*") in advance of the return of Née. In volumes 4 to 6 of the *Icones*, however (published 1797–1801), and in Cavanilles' *Descripciones* (1801–1802) there are a number of references to seeds brought (*allatis*, *adsportatis*) by Née and subsequently grown at the Garden. According to Cavanilles (Ic. 5: I–III. 1799) Née's herbarium resulting from the expedition amounted to 10,000 specimens, of which perhaps one-third represented new species. It is not surprising that references to Née and to his herbarium became more and more frequent in the later volumes of the *Icones*.

Luis Née, about whom relatively little seems to be known, travelled widely with the Malaspina expedition. His herbarium included plants from many parts of the world. His Mexican specimens were obtained chiefly in the course of a journey with a party that left Acapulco in May 1791 and returned in December of the same year, having visited Mexico City, the mining regions of Hidalgo, Querétaro, and Guanajuato (Engstrand 1981; cf. also Syst. Bot. 7: 234–235. 1982). Née is known to systematists chiefly for his paper on Mexican oaks (Née 1801), one of the earliest published revisions of any genus of Mexican plants. His herbarium has been carefully conserved (but little used) in Madrid. When Pavón was selling specimens from the Peruvian expedition and from the Sessé & Mociño expedition, as described later on in this paper, he informed Philip Barker Webb (in a letter, 7 July 1826) that he was unable to furnish him with any of Née's duplicates because the entire collection was being kept at the Garden for future study and publication: "En cuanto a las Encinas, Chenes o Quercus del Norte de M^r. Née el q^o. viaje con Malaspina, esta coleccion se conserva en el Jardin botanico de Madrid con todas sus colecciones botanicas par publicarlas al dia por orden de mi Rey de España."

Returning to the *Icones* of Cavanilles, it may be seen that the second volume included 16 newly described Mexican species. The first 53 plates were ready for the engraver early in April 1792 (letter, Cavanilles to de Jussieu, 30 October 1792), and probably all the plates were finished well before the end of 1793 (for publication up to a year later), so it may be supposed that most of the Mexican species came from seeds supplied by Sessé or Cervantes, though Cavanilles is consistently silent about this. As noted above, some Mexican materials may have reached Madrid from the Malaspina expedition about the middle of 1792.

Half of the third volume of the *Icones* is devoted to newly described Mexican plants grown in the Madrid Garden. Species in the early part of the volume, said to have flowered in 1793, may well have come from Sessé or Cervantes, whereas those in the latter part, with dates of flowering given as from May–July 1794 to August–September 1795, may well have been contributed by Née. At present there is no way to be sure. Beginning with the fourth volume (1797–1798) Cavanilles described more and more species from the herbarium of Née, and fewer Mexican species from garden-grown plants (in volumes 4–6, respectively, the numbers of such species are 26, 9, and 0).

In the first three volumes of the *Icones*, Cavanilles rarely mentioned any specific localities from which seed had come and only exceptionally mentioned the sender. Even in the later volumes, and perhaps in the earlier volumes as well, it seems in some instances that Cavanilles at the time of publication did not know the source of the seed, but in subsequent publications gave the credit to Née. In the fourth volume Née is often mentioned, but rarely in such a way that he may

be positively identified as the collector of the original seeds. Of *Tagetes micrantha*, for example (plate 352), Cavanilles says it flowered in the Garden in October 1796, and he says it was "observata" by Née near Querétaro, but he does not say in so many words that Née *collected* it near Querétaro. I suspect that in many or most instances Cavanilles did not know the original sources of the seeds from which plants were grown at the Garden. Because of the strained relations between him and Ortega, I surmise that Cavanilles was free to study the plants as they grew in the Garden, but not the Garden's records of accessions, if indeed any careful records were kept.

Incidentally it may be noted that Cavanilles published (Ic. 4: 70–71. 1798) a list of the species published in the *Icones* up to that time, for which Née could supply definite localities. These localities may or may not represent the original localities of the species described by Cavanilles. Certainly for species described in the first volume (the species enumerated by Cavanilles as nos. 1–109) they do not, as these species were grown in the Madrid Garden no later than 1790 or early 1791, before Née was ever in Mexico. The localities are in fact those at which Née collected (or observed) species that Cavanilles assumed to be the same species he himself had described earlier without knowing exactly where they had come from.

For species published in the later volumes of the *Icones*, however, Née's localities as published by Cavanilles may indeed represent the actual sources of the material later grown in the Madrid Garden. The data supplied by Née often confirm the suppositions made independently by later students, as to the identities and actual geographical sources of Cavanilleian species. For example:

Aster glutinosus Cav. Ic. 2: 53. *pl.* 168. 1793. Supposed by Cavanilles to have come from Mexico; flowered at Madrid in December [1792 or earlier]. Steyermark (Ann. Missouri Bot. Gard. 21: 586–588. 1934), after study of supposed type-material, stated that this was a species of limited distribution in Peru and Chile. Née (Cav. Ic. 4: 71) gave the locality as "in Peruvia iuxta Arica haud procul a mari".

Ipomoea pentaphylla Cav. Ic. 3: 29. *pl.* 256. 1795. Grown at Madrid from seeds sent by the Malaspina expedition, the original locality unknown to Cavanilles at the time of publication. In 1798 (Cav. Ic. 4: 71), Née's locality was given as "in fundo Calavan insularum Philippensium".

Malva miniata Cav. Ic. 3: 40. *pl.* 278. 1796. Flowered at Madrid in July 1795, at which time the source of the seed was unknown to Cavanilles. Later (Descr. 168. 1801) he ascribed it to "Queretaro y otras partes de Nueva España", apparently overlooking the fact that in Ic. 4: 71. 1798 he had stated that Née found it "in Talcahuano urbe Regni chilensis". The species, now called *Sphaeralcea miniata* (Cav.) Spach, is generally conceded to be South American.

Guazuma polybotrya Cav. Ic. 3: 51. *pl.* 299. 1796. The type-locality is given as "New Spain", but Cavanilles later (Ic. 4: 71. 1798) says Née found the species "in insula Taboga, et inter Guayaquil et Guaranda". This confirms the conclusion to be drawn from Cavanilles' original description, which suggests his plant was *Guazuma ulmifolia* Lam., not the common Mexican species, *G. tomentosa* H.B.K.

On the other hand there are certain contradictions in the list of Née's localities published by Cavanilles, and botanists should interpret each one on its own merits:

Encelia halimifolia Cav. Ic. 3: 6. *pl.* 210. 1795. The type locality was given as "New Spain"; later Cavanilles (Ic. 4: 71. 1798) stated that Née found it "ab

oppido mexicano Real del monte usque ad fundum de Regla". According to modern interpretation this is a species of limited distribution in Sonora and Baja California.

Oxalis tetraphylla Cav. Ic. 3: 19. *pl.* 237. 1795. The type locality was given as Mexico. Most botanists have interpreted this as a Mexican species, but Cavanilles (Ic. 4: 71. 1798) states that Née found it "in Madalena oppido peruviano inter Batatas".

Oenothera tetraptera Cav. Ic. 3: 40. *pl.* 279. 1796. The type locality was "In Sotoluca Novae-Hispaniae". Later (Ic. 4: 71. 1798) Cavanilles stated that Née found this species "in fundo de Gonzales", 7 leagues from Querétaro.

Née's locality-data are provided for only a little more than half the Mexican plants described in the third volume of the *Icones*, and for fewer than one-third of the new garden-grown species described in the fourth volume. It may be supposed that the new species that are *not* listed, were not found by Cavanilles among Née's collections nor recognized by Née as something he had seen in New Spain. The probable alternative is that these species were grown from seeds supplied by Cervantes or Sessé; the list of these last includes:

Vol. 3	<i>Ipomoea tricolor</i>	<i>Ruellia lactea</i>
	<i>Aster pinnatus</i>	<i>Solanum triquetrum</i>
	<i>Milleria angustifolia</i>	<i>Dahlia rosea</i>
	<i>Pteronia porophyllum</i>	<i>Dahlia coccinea</i>
	<i>Anthericum reflexum</i>	<i>Coreopsis heterophylla</i>
	<i>Cineraria praecox</i>	<i>Bignonia? linearis</i>
	<i>Solanum lanceolatum</i>	<i>Cerbera ovata</i>
	<i>Rudbeckia perfoliata</i>	<i>Verbesina virgata</i>
	<i>Siegesbeckia triangularis</i>	<i>Ceanothus macrocarpus</i>
	<i>Coreopsis ovata</i>	<i>Galinsoga trilobata</i>
	<i>Aeschynomene virgata</i>	<i>Mimosa distachya</i>
	<i>Rauwolfia glabra</i>	
Vol. 4	<i>Solanum lentum</i>	<i>Psoralea lutea</i>
	<i>Solanum fructu-tecto</i>	<i>Stevia serrata</i>
	<i>Sida bicolor</i>	<i>Mirabilis corymbosa*</i>
	<i>Sida linearis</i>	<i>Cuphea procumbens*</i>
	<i>Aralia humilis</i>	<i>Psoralea mutabilis*</i>
	<i>Aeschynomene picta</i>	<i>Oenothera rubra</i>
	<i>Aeschynomene longifolia*</i>	<i>Virgilia secundiflora*</i>
	<i>Salva circinata</i>	<i>Ruellia ocymoides*</i>
	<i>Salvia papilionacea</i>	<i>Sida disticha</i>
	<i>Salvia phlomoides</i>	<i>Mirabilis aggregata*</i>

The asterisk (*) indicates species subsequently described by Ortega under another name, from material sent to the Garden by Sessé.

From the standpoint of modern taxonomy it is interesting to note that Cavanilles' judgment on what constituted a species was sound; for about four-fifths of the plants he described, the names he proposed are still in use. When it is remembered that some of the remaining names were later homonyms and so unusable, his percentage is even higher. On the other hand, Cavanilles was conservative in his outlook on genera. It is true that he described a number of new genera, but in the judgment of later botanists he could have described many more; of all the species currently passing under the specific epithets given them by Cavanilles, almost exactly one-half are now assigned to different genera from those in which he placed them. Familiar examples are *Chelone* (now *Penstemon*);

Malva (*Malvastrum*, *Sphaeralcea*); *Mimosa* (*Acacia*), *Psoralea* (*Dalea*), *Asclepias* (*Cynanchum*, *Gonolobus*), *Aster* (*Grindelia*, *Dyssodia*), etc.

Apparently the Madrid Garden was receiving new accessions from Mexico fairly frequently during the mid-1790s. For example, *Solanum fructu-tecto* Cav. (Ic. 4: 5. 1797), flowered in Madrid in the autumn of 1796. Cavanilles said of its origin, "In Imperio Mexicana. Culto in R.H.M. ex seminibus inde missis". The implication is that the seeds were sent from Mexico about 1795, thus presumably by Sessé or Cervantes. As noted above, Cervantes was sending appreciable quantities of seeds as late as 1803. Perhaps stimulated by new accessions, or for other reasons, and more than five years after Cavanilles began to publish his *Icones*, Ortega began, a little too late, what must have seemed a competitive effort to catalogue and describe the plants in the Royal Garden. Perhaps he felt it was politically necessary to preserve his standing vis-a-vis Cavanilles. I prefer to think that a large new shipment of seeds, or perhaps more than one shipment, must have been received from the New World, perhaps in the spring of 1796, when Sessé had been exploring in Cuba.

In 1797 Ortega began the publication of his *Novarum, aut rariorum plantarum Horti Reg. Botan. Matrit. Descriptionum Decades* in which he ultimately described 100 species grown in the Garden. The first four *Decades* were issued as a unit in November 1797. In these pages Ortega described more than 30 new species from Mexico (or, as he often, but usually erroneously, supposed, Cuba), almost all grown from seeds sent ["*missis*"] by Sessé. The months of flowering are given for most species; these range from July to December for the most part, but the dates for a few (e.g., *Maurandya semperflorens*, are given as from July to February). It is possible that all the descriptions are of plants cultivated in the Garden in former years and only now described, but it seems more likely that the impetus for publication was provided by a considerable accession received in 1796 or earlier.

More than half of the new species described between 1797 and 1800 in the ten *Decades* (actually 53 out of 100) were based on plants grown at the Garden from Sessé's seeds. Material of a few Mexican species had been supplied by Cervantes or by one of his students in Mexico, Don Antonio Cal of Puebla. A few South American and at least one Mexican species (*Aeschynomene miniata*) were raised from seeds brought home ["*allatis*"] by Née. Nine species, said to have been Cuban in origin, are credited to Espinosa, to Boldó or to Jos. Guio, all of whom had taken some part in recent West Indian explorations. The remainder included South American material from Ruiz & Pavón, some specimens received from the Marchioness of Bute, and a few species of unstated origin.

Many of the plants supposed by Ortega to have come originally from Cuba were in fact Mexican in origin, but apparently most of the "Cuban" species attributed to Guio (cf. Cavanilles, *Icones* 4: 49) (e.g., *Phaseolus microspermus*), to Boldó (*Salvia bullata*), or to Espinosa (*Crotalaria pumila*, *Celtis epiphylladena*, *Ipomoea sinuata*, *Rhus lineatifolium*, and *Solanum ficifolium*) were Antillean. On the other hand *Echeandia terniflora*, supposedly grown from Cuban seeds sent by Espinosa, is presumably a Mexican plant, and *Malva* [*Sida*] *leprosa* is not known from Cuba.

So many of the "Cuban" species attributed to Sessé are known today to be of continental rather than Antillean origin, that it seems likely that there was some error in labelling seeds. Most of the "Cuban" species published in the first *Decades* were said to have flowered in the period from July to October. If these were the

summer and autumn months of 1796 (allowing Ortega a year in which to prepare the text and have the engravings made for publication), then presumably the seeds must have been received in Madrid no later than the spring of 1796, and may well have been sent from the New World during the winter of 1795–1796. Sessé was in Cuba at this time, somewhat overextended in his efforts to secure a passage to Mexico for himself and his collections (Rickett 1947), and it is easy to imagine the possibility of some error. Sessé may have sent seeds to Ortega directly, or through Cervantes in Mexico. He may have carried some Mexican seeds to Cuba with him, intending to send them to Spain at the first opportunity; it is conceivable that Ortega, on receiving a package from Cuba, assumed the contents of the package had originated in that island. Or perhaps Cervantes in forwarding a mixed lot of Antillean and Mexican seeds, failed to separate them adequately. We shall probably never know the truth of what happened, but botanists should be cautious in citing these species from Cuba on the basis of Sessé's collections alone.

It is probable that most of the living plant material sent to Madrid by the Royal Botanical Expedition lacked complete documentation. Locality data are almost completely wanting in the herbarium specimens collected by the expedition, and there is no reason to suppose that living plants, including seeds, were more carefully labelled. Probably seeds were sent in bundles containing small lots of a number of species, without any proper indication of origin, so that when the material was received in Madrid it was planted with the understanding that it came from "New Spain". It may be supposed that when either Ortega or Cavanilles studied a certain plant in the Garden, neither one of them knew exactly where it came from except in special circumstances.

The estrangement between Ortega and Cavanilles, that seems to have resulted in almost complete lack of communication about plants in the Garden, now seems comic in a way but had some serious implications for future botanists, because the two men repeatedly described the same species, and probably the same plant, under different names. About half the new species of garden-grown Mexican plants in the fourth and fifth volumes of Cavanilles' *Icones* (1797–1799) probably came from seeds sent by Cervantes and Sessé. During the same period Ortega was describing more than 50 species definitely attributed to Sessé. Cavanilles (Ic. 4: 72. 1798; 5: 70. 1799; 6: 82–83. 1801) acknowledged that 32 of Ortega's new species were identical with species he himself had published. In some instances Ortega acknowledged the synonymy. All this might seem but a comedy of errors, except that the precise dates of publication of Ortega's *Decades* are not all known, and determination of priority of competing names is not always possible. Reference to the literature cited at the end of this paper will show that volume 4 of the *Icones* was published between September 1797 and May 1798, and *Decades* 1–4 in 1797 according to the title page and surely before September 1798. *Decades* 5–6, published 1798 but the exact date unknown (presumably May–December), possibly may compete with the fourth volume of the *Icones*. Names published in *Decades* 7–8 date from 29 January 1799, according to a contemporary note by Cavanilles, and therefore have priority over those published in the fifth volume of the *Icones* (April 1799).

Whatever the complications, Cavanilles and Ortega between them, up to about 1801, described approximately 250 new species of plants as a result of material sent to Madrid by the Royal Botanical Expedition in New Spain. All this while the expedition was still in the field. It must have seemed like a promising beginning.

Sessé returned to Madrid in 1803, and brought with him a large number of seeds for the Royal Botanical Garden, as well as great quantities of other botanical spoil from the New World. Cavanilles saw the collection, and reported enthusiastically to J. E. Smith (letter, 6 April 1804) that Sessé thinks he has 4000 plants, "dont la plus grande partie est dessine a merveille. Quelle cantite des genres nouveaux! Nous pouvons deja dire Voicy l'embarras des richesses!" Unfortunately Cavanilles could not take advantage of this opportunity. He died a month later (4 May 1804) and was succeeded by Francisco Zea (1770–1822), Ortega having been retired in 1801 on full salary. During Cavanilles' short tenure he had made substantial improvements at the Garden. The number of species cultivated had increased from 3000 to 7500. After his death (Steele 1964, p. 245) the Garden maintained a Cavanillesian tone, thanks to the enthusiasm generated among his students, who one time are said to have numbered two hundred. In spite of continued activity at the Garden, hardly a significant publication dealing with Mexican plants came from there in more than a decade.

Zea having served the Garden during a difficult interregnum, he was followed as director by Mariano Lagasca (1776–1839), who had been a favorite pupil of Cavanilles. Lagasca had been named Professor of Medical Botany at the Garden in 1807 (Colmeiro 1858, p. 192), then during the wars with the French served in the army, and apparently returned to Madrid about 1813. Lagasca was a talented botanist who was unlucky. In the midst of political unrest in Spain he lost his herbarium and manuscripts and eventually was forced into exile in England. During the first and second decades of the century, however, while he was connected with the Madrid Garden, he published occasionally on the plants that had been received from New Spain. He was interested in grasses, and his memoir on the new American genus *Bouteloua*, based largely on specimens sent by Cervantes and Sessé, appeared in a Spanish periodical (Lagasca 1805). His best known contribution came more than a decade later.

Sessé, after his return in 1803, had turned over the Royal Botanical Garden a number of seeds that were successfully grown. In a thin volume that was essentially a list of the plants cultivated in the Garden in 1815, with descriptions of some of the new or more interesting species (Lagasca 1816), Lagasca made many references to the contributions of Cervantes, of Sessé, and of their colleague who had joined the expedition in 1790, the Mexican botanist José Mariano Mociño. Approximately 57 species are credited to Sessé, Mociño, or Cervantes, and more than 40 others are cited as from New Spain or Mexico, without further indication of the source; all these are in addition to the 20 or more Mexican species attributed to Née. A few references are to plants sent by Sessé in 1803 (e.g., Lagasca, 1816, p. 10, *Physalis foetidissima*), but most are to seeds received by the Garden in 1804, e.g., *Salvia melissodora* (ibid., p. 2), "Intr. ann. 1804 ex seminibus à cl. DD. Sessé et Mozinno ex N.H. advectis."

Contributions to the Madrid Garden and to other gardens in Europe continued to trickle in from Mexico as long as Cervantes was associated with the Botanical Garden there, but because of political unrest both in Spain and in Mexico the total amount may have been relatively small. Lagasca mentioned a half dozen species received from Cervantes in 1814, and, as noted above, there is a record of a sizeable shipment of seeds from Cervantes in 1815. Even as late as the year of his death (1829) some material was being received in Europe. Link and Otto, for example (Ic. Pl. Rar. 43. pl. 22. 1829) attributed the name *Doronicum mexicanum* to Cervantes and stated that the seeds had been obtained from him by the collector Deppe.

Cervantes seems also to have made a significant contribution to the first modern botanical work published in Mexico, the *Novorum Vegetabilium Descriptiones* (1824–1825) of Pablo de la Llave and Juan Lexarza. He is credited in the pages of that work with the authorship of at least 5 new genera and 13 new species, and his continued support and encouragement are gratefully acknowledged by LaLlave.

In summary, it seems that after due allowances for duplication and ambiguity, Spanish botanists between 1791 and 1816, and even up to 1825, based the names of more than 250 or as many as 300 new species and many new genera upon materials that had been discovered and contributed by members of the Royal Botanical Expedition. This was only the first stage of the activity involving the physical legacy of the expedition. The publication of a great sumptuously illustrated *Flora Mexicana*, long envisioned by Sessé and his colleagues, had become an impossibility, and the chief botanical members of the expedition had passed from the scene. By the time of publication of Lagasca's *Diagnoses* in 1816, Sessé had been dead for almost eight years, Cervantes was isolated in Mexico and caught up in the turmoil of revolution there, and Mociño was in exile in France.

DISTRIBUTION OF PLANTS FROM THE MADRID GARDEN 1790–1815

It should be emphasized, though it has already been implied, that most of the plants of "New Spain" that were proposed as new species by the Spanish botanists while the Royal Botanical Expedition was in the field, that is, until 1803, were described from living plants grown in the Madrid Garden. The primary exceptions to this are the species based on specimens in Née's herbarium, to which Cavanilles had access after 1794. The herbarium of Sessé & Mociño was not available in Europe until after 1803, and was little used in the years immediately following, because of the death of Cavanilles, the illness and death of Sessé (in 1808), and the disruption caused by the Napoleonic wars.

The Royal Garden continued its activity, as noted above, and as many plants from tropical America thrived in Spain, it was only a few years before their seeds were being widely distributed. In 1803, the year Sessé & Mociño returned to Spain, the Madrid Garden harvested 7649 packets of seeds, which were distributed to public gardens or to correspondents ("a los Profesores") in "Paris, Londres, Stokholmo, Copenhagen, Nimes, Mompeller, Portugal, Viena, Turin, Pavía, Florencia, Génova, Parma, Filadelfia, Cartagena, Sevilla, Burgos, y Peru" (Cav. Anal. Ci. Nat. [Madrid] 6: 330–331. 1803). When second-generation Mexican plants began to flower in other gardens, this set off another wave of descriptions of new species. The effects of such wide dissemination of seeds, and the botanical studies that have ensued, have been profound in botany and in horticulture.

Many species first described from the Madrid Garden appeared with almost incredible rapidity in gardens elsewhere in Europe. Standard sources listing the dates of introduction of cultivated plants into England show that *Tagetes tenuifolia* was introduced in 1795; *Zinnia elegans* in 1796; *Piqueria trinervia*, *Dahlia coccinea*, *D. pinnata*, and *D. rosea*, and *Tagetes lucida* in 1798; *Cosmos bipinnatus*, *C. sulphureus*, and *Zinnia tenuifolia* in 1799; and *Bidens heterophylla* (published in 1799) in 1803.

Sometimes the link with New Spain through the Madrid Garden was very tenuous. In 1793, for example, Jacquin published the name *Zinnia elegans* for a plant cultivated in Vienna, the original source unknown to him. He did not say

where he obtained the seed, but stated that he had received it as he published it, under the name *Zinnia elegans* ("sub hoc titulo semina accepi"). It must be more than a coincidence that *Zinnia elegans* was the name by which the plant was known to Sessé & Mociño (and under which it was published in their posthumous work in 1890). I can only assume that seeds were sent to Madrid under this name, and the progeny distributed under the same name, perhaps by Ortega as early as 1790. In the meantime, in 1791, Cavanilles had given another name to the same species, apparently from plants that flowered in Madrid in 1790, so *Zinnia elegans* is of academic interest only.

The Madrid Garden was still carrying on active exchanges a decade or more after the death of Cavanilles. The number of species and varieties grown in the Garden in 1815, according to Lagasca's *Elenchus* (1816), was between 3500 and 3600. Seeds of 1700 taxa were offered in exchange. The offerings included more than 40 of those that were being newly described at the same time, from New Spain. About 30 were attributed to Sessé or to Mociño, or to Cervantes. Most of them had been grown in Madrid since 1803 or 1804. In the same list the Garden offered in exchange the seeds of about 100 species described by Ortega and Cavanilles, most of them Mexican, many of them also derived from seeds supplied by Sessé and his associates.

Thus by the year 1815 the Garden had been for more than a decade, and perhaps for twice that long, an established source of plant material from New Spain. Through its exchanges it started a wave of horticultural activity that has not yet subsided. When one opens a modern nursery catalogue and sees the hundreds of varieties of dahlias or zinnias offered for sale, he is seeing one of the legacies of the Royal Botanical Expedition. Many of the common and conspicuous plants of Mexico, especially those of the mountains and uplands easily accessible from Mexico City, were first described and figured in the *Icones* of Cavanilles. Such genera as *Cobaea*, *Cosmos*, *Dahlia*, *Franseria*, *Heterosperma*, *Lopezia*, *Nocca* [*Lagascea*], *Milla*, *Piqueria*, and *Stevia* were first described by him. He also indicated through his descriptions and illustrations something of the remarkable richness of the Mexican flora in such genera as *Dalea*, *Salvia*, *Solanum*, and *Zinnia*. It is abundantly clear that most of the information about these primarily montane genera, and most of the original seeds, came from material sent to Spain by the Royal Botanical Expedition. No other group was in Mexico long enough at this period to have obtained such a wide variety of viable material.

I cannot expand here upon the horticultural implications of this story. As far as I am aware they have not been belabored. It would be fascinating to trace the development of the cultivars of *Cosmos*, *Dahlia*, *Salvia*, and *Zinnia* through European gardens after their introduction from Mexico. It is enough to say that Sessé and his coworkers did make a real contribution to our gardens as well as to the contemporary gardens of Europe.

Perhaps inevitably there were complications and some abuses in the wake of rapid and widespread distribution of plant material from Madrid. Much of the material seems to have been handled in what would now be considered an inexcusably slipshod manner. As noted above, seeds and other plants may not have been accompanied by adequate locality data when they came to Madrid from the New World. Perhaps other gardens receiving seeds from Madrid failed to record the source of the material when the seeds were planted. Perhaps part of the blame belongs to the early 19th century, a time when interest in plant geography was minimal. Whatever may have happened, the recipients of the seeds soon began

describing the plants as new species after they flowered in their own gardens. Usually they neglected to mention Madrid as the source of the material; perhaps sometimes they did not know the original source, having received third- or fourth-generation seeds from Paris, Berlin, or Montpellier. Sometimes they provided new names for species already described in print by Ortega or by Cavanilles.

The situation was complicated, because at the beginning of the 19th century it was still a marginally acceptable practice to provide valid names for plants by describing them in public lectures. Unfortunately names thus given locally (as in Spain) did not always find general acceptance because people in other countries were unaware of their existence. It was not uncommon for botanists in other parts of Europe, on receiving seeds from Madrid, to publish the accompanying names as if they were new, not understanding that the names had been attached to the plants for years, after demonstration by public lecture.

Lagasca (1816) alluded to this situation in the foreword to the *Elenchus*; for the following lively translation I am indebted to Michael McVaugh: "This list of plants in the Garden in 1815 is much smaller than the lists that were prepared in 1805 and 1806. A great many of the plants cultivated then are no longer in the Garden, and we bitterly regret their loss due to the war. But the seeds of these (named, unless I am mistaken, according to the proper rules), were taken by the famous gardens of Europe. The names assigned to them in the Royal Gardens of Madrid by the wisest professors have very often been kept by the public, as can be seen in the very recent Catalogues of the Garden of the Academy of Torino, of the Royal Garden in Munich, and also in the Hortus Hafniensis published by the celebrated Hornemann in 1815. Yet I know not by what ill chance, the Royal Madrid Botanical Garden, which first sent out the seeds, is scarcely ever mentioned in them, and the honor is first given to other Gardens, to Berlin and Montpellier particularly. Far be it from me to suppose this was done intentionally."

Lagasca goes on to say, "these plants were not only named by us but for the most part described, a number of the more difficult in 1805, and all in 1806 and 1807 in public lectures. I have felt it necessary to say this here, lest I seem to do an injury to someone when I retain plant names first given by the Royal Garden of Madrid."

Lagasca's grievance was not an unreasonable one. Certainly under any circumstances it would have been the courteous thing to acknowledge the part played by the Madrid Garden, if indeed this information was available. The present problem, however, is not so much the nebulous one of credit where credit is due, but the very practical one of identifying names that were published without proper documentation. No one knows exactly how many species were published in this way, mostly in garden catalogues between 1800 and 1815, by Balbis, de Candolle, Hornemann, Jacquin, Nocca, Schrank, Willdenow, and others. For example, there is often a strong inferential link between plants of the Sessé & Mociño expedition, and items in such garden catalogues as Balbis' *Catalogus stirpium horti bot. Taurinensis* (83 pp., 1813), and Hornemann's *Hortus regius botanicus Hafniensis* (2 vols., 1813–1815), but seldom can a direct connection be established.

Lagasca (1816) published the name *Asclepias virgata*, in the modern way with a diagnosis. The plant had been cultivated in Madrid, under the same name, since 1804. We may guess that *Asclepias virgata* Balbis (1813, p. 14) is the same, but it seems impossible to be sure; the link has been lost. Sometimes Lagasca himself

was not sure of the link; in 1816 he queried whether his newly published *Salvia lanceolata*, grown at Madrid since 1804, was the same as *S. lanceolata* Hornem. Hort.-Hafn. p. 32.

One of the more interesting problems raised by the study of the botanical results of the Royal Botanical Expedition is this of the indirect connection between the expedition and these garden catalogues of a few years later. It may be impossible to prove a direct connection for any one species. Starting with the idea that there *should* be a connection, however, one may be able in many instances to work back through correspondence, garden records when such exist, and types and other specimens, to forge direct links.

EARLY DISPERSAL AND UTILIZATION OF THE SESSÉ & MOCIÑO HERBARIUM

As mentioned above, the herbarium was not available to Ortega, nor to Cavanilles. It was returned to Madrid with the expedition, and was subject to some reorganization and study, probably until the death of Sessé in 1808. It was used by Lagasca, whose handwriting appears on many of the specimens. After the interruption caused by the war, while Mociño was still in exile near Montpellier, there began a strange series of events that led to the depletion of the herbarium in Madrid, and at the same time made the specimens available to European botanists, as they would not have been had they remained in Madrid.

José Antonio Pavón (1754–1840), who with Hipólito Ruiz (1754–1816) had participated in the Spanish expedition to Peru and Chile (1777–1788), after returning to Spain had worked hard and long to further the publication of the *Flora Peruviana et Chilensis*. By the year 1814 support for the *Flora* had dwindled to nothing. Pavón, without government support and desperately in need of money, began to sell specimens that had been gathered by the Peruvian expedition, and also specimens from the expedition to New Spain. The story is told in detail by Steele (1964). The specimens had been collected on government-sponsored expeditions, and presumably belonged to the State, not to Pavón. Apparently no one cared enough to be very strict about this, though in correspondence he confided that he could not sell duplicates from the collection of Née, or duplicates of Triana's collections from Nueva Granada, because they were securely under the control of the Botanical Garden (letter to Philip Barker Webb, FI). The question of Pavón's probity was raised by the authorities but the matter was eventually dropped. By that time the specimens had been sent out of Spain, beyond any possibility of retrieval, and botanists elsewhere in Europe soon became aware of them.

Apparently it all began when Pavón received a letter (May 28, 1814) from Aylmer Bourke Lambert, a British botanist and collector of considerable means and talent, asking to buy herbarium duplicates, insects, and other natural history specimens. Pavón's letters to Lambert over the next 11 years number about 160, bound in a volume entitled "Letters, A.B.Lambert, Esq." in the library of the Royal Botanic Gardens at Kew. Pavón first wrote to Lambert on August 12, 1814, offering him 1500 American plants, "each with its label." Apparently this first shipment was not sent until about the end of March, 1816. Lambert received them in July and was much pleased with his bargain. Insects sent at the same time went to Alexander MacLeay, secretary of the Linnean Society. Over the next few years trading continued. Pavón sent herbarium specimens, samples of bark and

wood, and sea shells. Lambert returned money, and botanical publications needed by Pavón, who was isolated from the international botanical community. It appears from the Lambert letters at Kew that Pavón sent Lambert, between 1816 and 1820, at least 6000 and perhaps as many as 10,000 plants, mostly from America but including some from Spain. Pavón's letters do not always make it clear which shipment is going out, and how many specimens are involved.

After 1820 the trade with Lambert slowed to nothing. The last letter from Pavón at Kew is dated July 18, 1825. Pavón was more than 70 years old and still in need of money. He negotiated in 1825 and 1826 with A. P. de Candolle, without success, even though he offered to sell plants to de Candolle for less than the amounts that Lambert had paid for them. He sold some specimens to other European botanists; Moïse Etienne Moricand (1779–1854), de Candolle's friend, wrote to the latter on September 8, 1827, that he had received 800 specimens from Pavón.

Fortunately for Pavón, he was able to establish a profitable trade with another wealthy British collector, Philip Barker Webb (1793–1854). Their dealings are documented by a series of letters, the "Webb Correspondence" at the Istituto Botanico at Firenze. Pichi-Sermolli (*Nuov. Giorn. Bot. Ital.* II. 56: 699–701. 1950) says that Webb eventually received 4994 specimens, including 2345 from Nueva España, 56 from Cuba, and 34 from Puerto Rico. Pavón's shipments, not only to Webb but to Lambert, often included several or many specimens of the same collection. In one letter to Webb (29 January 1828) he enumerated among a total of 2684 "species", 243 duplicates, 60 triplicates, 6 quadruplicates, and 1 "multiplicada".

Almost without exception, the original collections of Sessé & Mociño were without any locality data. When Pavón distributed duplicates, it was his practice to provide with each collection a small handwritten label bearing the name of the plant and an abbreviated locality, usually either "Peru" or "N E" [for Nueva España]. The Latin names, when the locality is "N E," are often those that were used by Sessé & Mociño. I have seen no evidence that he ever supplied more than one label when a collection included more than a single specimen. Sometimes the recipients made up a general printed label for the unlabelled duplicates. Some of these, doubtless because of Pavón's known connection with the Peruvian expedition, bear the words "Herb. Pavon" and "Peru". As various historians have remarked, many plants supposed to have come from Peru because of their connection with Pavón's herbarium, came in fact from Mexico or the West Indies; where Pavón never collected. It is clear that many such plants came from the herbarium of Sessé & Mociño.

The residue of the Sessé & Mociño herbarium, some 8000 specimens, remained untouched and unstudied for a century. Most of the specimens that Pavón sold to Webb remain unstudied in Florence to this day. On the other hand, the specimens in Moricand's collection, and especially those that Pavón sold to Lambert, ultimately had a considerable impact on 19th century botany. More than 300 new taxa were based on these duplicates. A list of the names of the botanists involved in this activity sounds like a roster of the eminent taxonomists of the period: Baillon, Bentham, Boissier, Brongniart, A. de Candolle, Cassini, Choisy, David Don, George Don, Decaisne, Duchartre, Dunal, A. de Jussieu, Lindley, Nees, Mueller Argoviensis, Reichenbach filius.

There were a few problems. Lambert's herbarium was sold in 1842 at public auction, in 321 separate lots. Many of the larger items were bought by dealers for

resale to collectors. Few botanists were among the buyers, the one conspicuous exception being Robert Brown, who bought for the British Museum a large set, said to include 665 species of Mexican plants among other items sold by Pavón to Lambert. The fate of the larger series bought by William Pamplin and other dealers is still mostly a matter of surmise. David Don had stated some years earlier (actually in 1824) that the Lambert Herbarium included nearly 2000 Mexican plants (Lambert, Descr. genus *Pinus*, pp. 32–39). Probably the largest selection of Mexican plants from Lambert's herbarium is now at Geneva (G, from the herbaria of Delessert and the Boissiers). A large series from the herbarium of H. B. Fielding, originally from Lambert, is at Oxford University (OXF). Other specimens have found their way to Paris, Leningrad, Vienna, and New York.

The great illustrated *Flora Mexicana* for which Sessé & Mociño worked was never published. A preliminary floristic treatment and a series of their unorganized field notes were published a century after they were written, when much of the material in them was obsolete. In spite of this it cannot be denied that much of botanical value resulted from the Royal Botanical Expedition. Contemporary Spanish botanists found some 300 new species and many new genera among the things that were sent from New Spain and grown at Madrid. Living material distributed from the Royal Botanical Garden made a significant contribution to horticulture and to knowledge of the tropical American floras. Specimens distributed by Pavón provided the bases for the descriptions of more than 300 American taxa new to science. Not previously mentioned in this paper, but described elsewhere (McVaugh 1980), are the approximately 370 paintings that represent the types of new names proposed by A. P. de Candolle and his contemporaries between 1813 and 1850. Sessé & Mociño worked at a time in history when most of the tropical American flora was unknown, though they did not fully realize this, and they were probably well-served by the devious ways in which their specimens came into the hands of others who were prepared to recognize new species and new genera.

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SYNCHRONOUS DICHOGAMY IN A MEXICAN ANONILLO *ROLLINIA JIMENEZII* VAR. *NELSONII* (ANNONACEAE)

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Plants with hermaphroditic flowers may have temporal separation of pollen release and stigmatic receptivity. If this separation, termed dichogamy, is complete within a flower, autogamy cannot occur. If, in addition, anthesis within an inflorescence or plant is synchronized, opportunities for geitonogamy may be reduced or eliminated. Synchronous dichogamy is perhaps best known in the Umbelliferae, where both protandrous and protogynous species are known to exhibit various degrees of synchrony (Müller 1883; Cruden & Hermann-Parker 1977; Lindsey 1982). In *Peucedanum lubimenkoanum* no overlap of male and female stages occurs within the plant (Ponomarev 1961), but in other cases synchrony appears to break down with increasing inflorescence size or number. Synchronous protandry within individual floral axes also occurs in *Delphinium cardinale* (Grant & Grant 1968), but we have found no reports for other members of the Ranunculaceae. Species of the lauraceous genera *Aniba*, *Clinostemon*, *Licaria*, *Persea*, and *Cinnamomum*, as well as *Ziziphus spina-christi* (Rhamnaceae), display a more complex temporal separation of male and female stages, involving two genetically determined mating types (Stout 1927; Galil & Zeroni 1967; Kubitzki & Kurz 1984). In these woody taxa, synchronous flower opening is maintained throughout the plant.

More recently, a system in which synchronous dichogamy is maintained throughout the plant but which does not appear to involve genetically-determined mating types was described for *Eupomatia laurina* (Eupomatiaceae) by Endress (1984). Here we report a similar type of synchronous dichogamy in a Mexican anonillo tree, *Rollinia jimenezii* var. *nelsonii* R. E. Fries. This is the first documentation of this system for a member of the Annonaceae.

METHODS

Trees were observed at two sites in an area of tall evergreen forest (*selva alta perennifolia*) mixed with pasture land in southern Veracruz, Mexico, from 10 through 26 May, 1983, near the close of the dry season. At the first site, north of Catemaco near Playa Escondida, elevation ca. 50 m, trees were isolated individuals in pastures and on forest edges; at the second locality, the nearby Estación de Biología “Los Tuxtlas,” elevation ca. 100 m, trees occurred on forest edges. A voucher specimen from Playa Escondida has been deposited in the University of Michigan Herbarium (MICH).

When this study was made the trees were in the midst of their flowering season, as evidenced by the presence of buds, mature flowers, and young fruits. In addition, examination of herbarium material indicated that flowering regularly occurs from April through June. Two trees at Playa Escondida were selected for

detailed study of anthesis, and 10 flowers on one tree and 19 flowers on the second tree were marked as they opened in the late afternoon of 10 May, and were observed subsequently at 18:43–18:54, 19:44–19:54, 22:48–22:55, 04:54–05:03, 08:30–08:40, 12:15–12:26, 13:42–13:54, 15:10–15:40, and 17:00–18:30. Stigmatic receptivity was judged to have begun when the stigmas became shiny with secreted fluid, and to have ended when the stigmas darkened and the stigmas and styles abscised from the carpels.

To determine the proportion of female and male stage flowers within and among trees, pollen and stigma presentation on these two trees, as well as on ten neighboring trees, was recorded over a two-day interval (the second day of observation was necessary to ascertain that no overlap of stages occurred). To follow floral synchrony over a longer period of time, two trees at “Los Tuxtlas,” one from 15–26 May and the other from 17–26 May, were similarly observed. Data from these observations were recorded as the number of open flowers present on a tree, based on a morning and an afternoon observation each day. All flowers on the tree were observed in preference to following only a marked sample in order to avoid overlooking any asynchronous flowering.

RESULTS AND OBSERVATIONS

Trees of *Rollinia jimenezii* var. *nelsonii* are 6–10 m high and have flowers borne on short shoots, with 1–2 flowers in an inflorescence maturing at a time. The flowers have trimerous perianths (dimerous and tetramerous flowers occur occasionally) consisting of short triangular green sepals, an outer whorl of petals that bear laterally compressed winglike appendages, and an inner whorl of small ovate petals. The six fleshy petals are pale yellow with a red-purple patch at the base where they are fused to form a chamber around the numerous stamens and carpels. The stigmas are loosely united and form a cap approximately 1 cm in diameter over the carpels; following the female phase of the flower this cap abscises as a unit from the remainder of the gynoecium (Fig. 1).

Flowers on the two trees observed at Playa Escondida began to open around 15:00 on 10 May. Most stigmas in the sample became shiny and presumably receptive before 19:00 and all had reached this stage by 20:00. This change was accompanied by a sweet, yeasty scent, which grew progressively stronger until it began to dissipate around 23:00.

At 05:00 of 11 May the stigmas were still shiny and the floral scent reduced. Throughout the day, the floral scent again slowly increased and the stigmas, although still shiny, had begun to darken. By 14:00 the stigmatic caps had abscised and the anthers had begun to expand, although no pollen had yet been released. Anthers dehisced between 15:00 and 16:00; dehiscence was complete before the corollas dropped from the flowers between 17:15 and 19:00. Throughout this observation period no asynchronous flower opening was found on either tree.

The pattern of anthesis over a longer period of time is shown for two trees at “Los Tuxtlas” (Fig. 2). In both trees there was a pattern of alternate day flower opening, as for Tree I on Days 1–6 and Tree II on Days 1–4; thus each tree presented either only female stage or male stage flowers on those days. That this rhythm was not perfectly maintained, however, is shown by the opening of flowers on successive days in both trees (Days 7 and 10–11 for Tree I, Days 5–9 for Tree II).

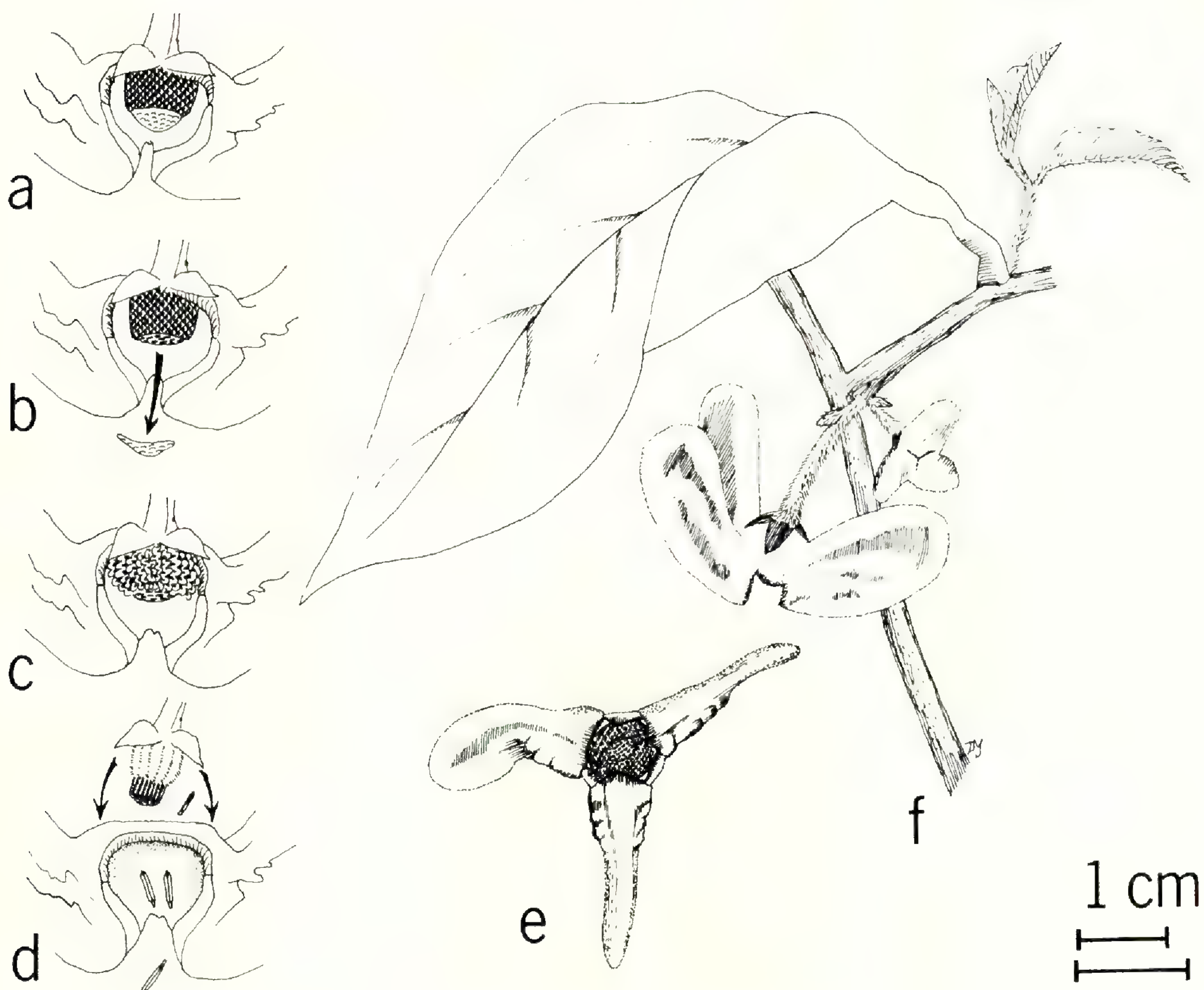


FIG. 1. *Rollinia jimenezii* var. *nelsonii*. a-d. Diagrammatic representation of the flower in lateral view with one outer petal and two inner petals removed. a. Flower during female stage of anthesis. b. Stigmatic "cap" abscission. c. Anther dehiscence. d. Fall of united petals. e. Apical view of flower. f. Habit. Large scale bar: a-d; small scale bar: e-f.

An indication of flower behavior within a small population on a single day is given in Table 1. The trees showed a pattern similar to that of the two individuals followed over a longer time period. Half of the trees had 100% female stage (3 trees) or 100% male stage (3 trees) flowers for that day, and nine of the 12 had more than 90% of their open flowers in the same stage (5 with >90% female stage flowers and 4 with >90% male stage flowers). During only two of 34 observations (Table 1, Tree II, and Fig. 2, Tree I, Day 7) were more than eight flowers of both sexual stages present on a single tree.

Nitidulid beetles were found in *Rollinia* flowers throughout anthesis, and it is probable that they act as pollinators. The beetles were small (ca. 4 mm long) and remained concealed within flowers for long periods of time rather than moving rapidly from flower to flower. Beetles were not marked, but the same number of individuals were found in the same marked flowers until the male stage was completed.

DISCUSSION

The flowers in *Rollinia jimenezii* var. *nelsonii* are strongly protogynous, with the stigmatic caps of all flowers abscising several hours before pollen release in

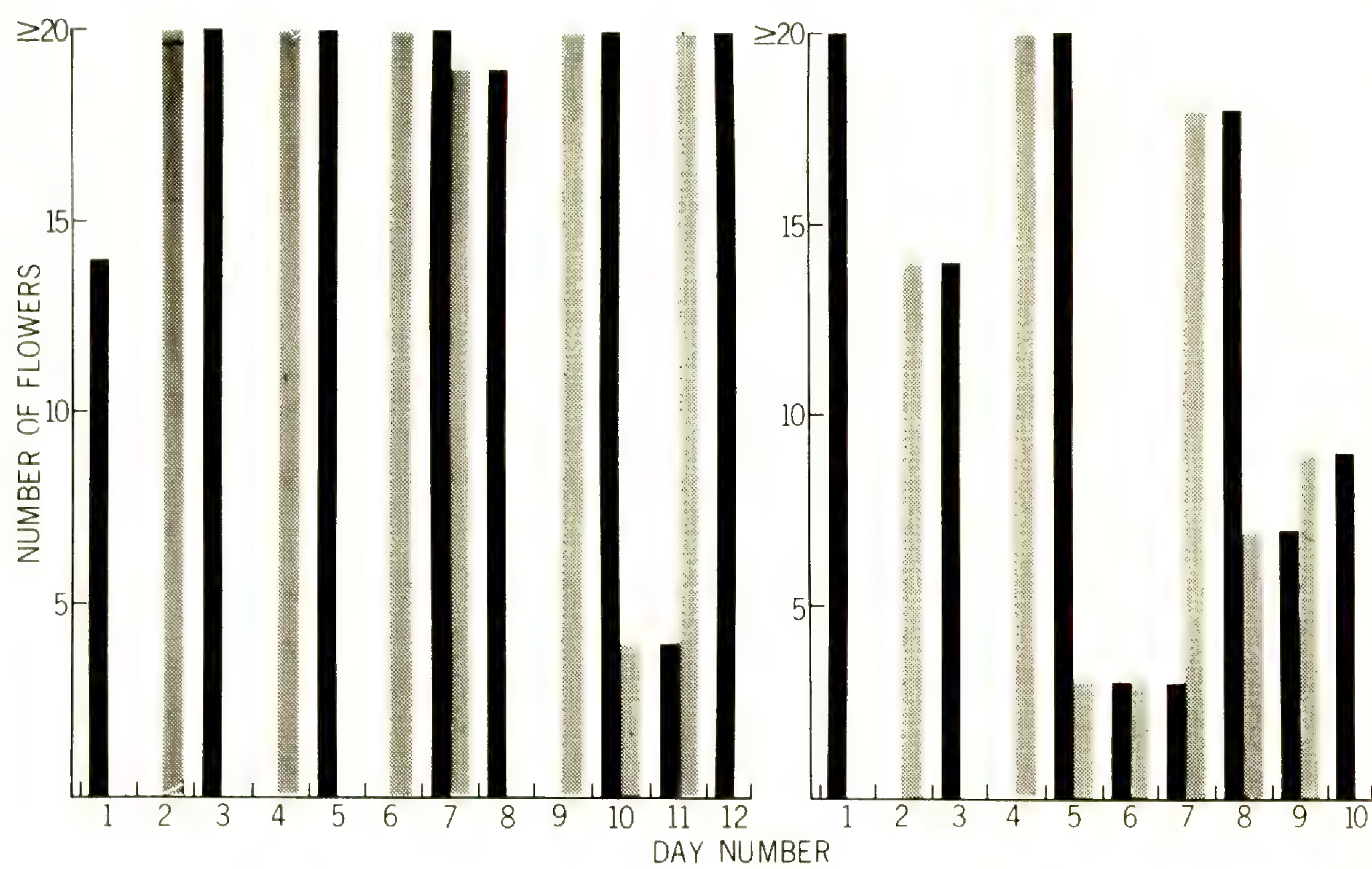


FIG. 2. Number of male stage (black) and female stage (shaded) flowers observed on two trees at “Los Tuxtlas” over a period of 12 days, 15–26 May (Tree I), and of 10 days, 17–26 May (Tree II).

Table 1. Number of female stage flowers and male stage flowers present on twelve trees at Playa Escondida on 11 May 1983.

Tree	number of female stage flowers	number of male stage flowers
1	0	>20
2	>20	>20
3	3	0
4	0	>20
5	18	0
6	>20	2
7	>20	1
8	1	>20
9	0	>20
10	>20	0
11	8	>20
12	8	7

the same flowers, thus eliminating opportunities for autogamous pollination. Events of anthesis are highly synchronous on a given tree and maturation of a new set of flowers usually occurs only once every 48 hours. Thus, floral behavior in *Rollinia* acts to limit opportunities for geitonogamous pollinations as well. Geitonogamous pollination is possible, however, when new sets of flowers open on a tree after only 24 hours; male stage and female stage flowers are then present simultaneously on the same tree. Periods of asynchronous anthesis also have the effect of changing the pool of potential outcrossing partners within a population.

Flowers are protogynous in many beetle-pollinated plants, with the beetles remaining inside the flower throughout anthesis. The beetles presumably enter the flower bearing pollen from a previous flower, deposit that pollen on receptive stigmas, and then pick up new pollen during the male stage. At this point the pollinator leaves bearing a fresh pollen load. This mechanism has been well documented for many Nymphaeaceae (Schneider 1979), *Magnolia* (Thien 1974), and *Calycanthus* (Grant 1950). *Rollinia* appears to have a similar mechanism, with nitidulid beetles acting as pollinators; nitidulids have been found in flowers of other genera of Annonaceae as well (Gottsberger 1970; personal observations).

If one assumes that *Rollinia* pollinators are unlikely to leave a tree while open flowers remain available, then synchronous dichogamy may serve to promote movement of beetles to a new plant when, following the male phase, few or no open flowers remain on the tree. In this way, floral behavior may increase the probability of cross pollination in *Rollinia*. A similar system may exist in species of *Annona* (Wester 1910; Webber 1981), but this has not been documented; other studies of floral behavior in Annonaceae (Kral 1960; Gottsberger 1970; Willson & Schemske 1980; Falcão et al. 1981; Norman 1982; Norman & Clayton 1986) have not mentioned such a system.

In contrast with *Rollinia*, herbs show an increase in asynchronous anthesis with inflorescence size and number. In *Delphinium cardinale* (Ranunculaceae) synchrony does not extend to the separate flowering stalks produced on larger individuals (Grant & Grant 1968); this was also found in the species of *Thaspium* and *Zizia* studied by Lindsey (1982) and in other members of the Umbelliferae as well. In this respect *Rollinia* is more like members of the Lauraceae and *Ziziphus spina-christi*, in which synchrony can be maintained throughout a large woody individual.

Synchronous dichogamy in the Lauraceae and in *Z. spina-christi*, however, involves two genetic morphs. For example, in the Lauraceae the first morph has receptive stigmas on the morning of Day 1 and releases pollen on the afternoon of Day 2; the second morph has receptive stigmas on the afternoon of Day 1 and sheds pollen on the morning of Day 2. This pattern was described by Stout (1927) in cultivars of avocado, *Persea americana*, but was also reported by Skutch (1945) from wild individuals of the related *P. caerulea*; more recently, Kubitzki and Kurz (1984) have found this pattern to occur in the Neotropical genera *Aniba*, *Clinostemon*, and *Licaria*, and in the Old World genus *Cinnamomum*.

There is no evidence that such genetically determined mating types occur in *Rollinia*. Theoretically, this allows crosses between all members of a *Rollinia* population since periods of asynchronous anthesis allow individuals to change their potential pool of "mates" within the population. The system in Lauraceae and in *Ziziphus spina-christi*, on the other hand, lacks this flexibility and is analogous to a diallelic self-incompatibility system in that the number of potential mates in a population is genetically determined and limited.

In addition to a lack of genetically determined mating types, *Rollinia jimenezii* var. *nelsonii* shares with *Eupomatia laurina* strong separation of sexual stages, synchrony of anthesis within individuals, and rhythmic production of open flowers (Endress 1984). In addition to these similarities, both taxa also have abscission and drop of accessory floral parts shortly after anther dehiscence. In the case of *E. laurina*, these are the basally fused stamens and staminodes; in *R. jimenezii* var. *nelsonii*, they are the connate petals. The occurrence of such a syndrome of characters in these two closely related families (Eupomatiaceae and Annonaceae) suggests that this type of floral behavior may be more common within the Annonaceae or other magnoliid angiosperms than is currently recognized.

Our data support the idea that synchronous dichogamy prevents autogamous pollinations and limits opportunities for geitonogamous pollinations in *Rollinia jimenezii* var. *nelsonii*. It is still necessary, however, to determine whether this floral behavior is maintained throughout the flowering season. Although this floral mechanism potentially influences pollinator behavior, details of the pollination mechanism are still unknown. It would be particularly useful to determine the effective pollinator and to relate pollinator movements to pollen flow and fruit set.

ACKNOWLEDGMENTS

We thank Dr. A. Estrada for permission to work at the Estación de Biología "Los Tuxtlas" and the entire staff for their assistance and hospitality. W. R. Anderson, B. Rathcke, W. H. Wagner, Jr., J. Webb, and S. G. Weller made helpful criticisms of earlier drafts of the manuscript. Field work was supported by a research assistantship from the University of Michigan Herbarium, and by a Cole Fellowship from the Department of Botany, University of Michigan, to N. Murray.

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TAXONOMIC NOTES ON *JUNCUS PELOCARPUS* S. L. (JUNCACEAE)

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The hexandrous bulbiferous rush *Juncus pelocarpus* E. Meyer occurs on open, gently sloping, sandy or peaty shores in soft-water habitats of eastern North America (Fig. 1), where water levels fluctuate over the course of the growing season. The plant produces rosettes of basally compressed leaves from creeping rhizomes, often forming extensive colonies. The culms bear diffuse inflorescences with flowers borne singly or in pairs (rarely in 3's). Flowers are often replaced by bulbils, small stiff fascicles of leaves, which may drop off and form new plants.

Engelmann (1866–1868), in the last complete revision of North American species of *Juncus*, treated three varieties of *Juncus pelocarpus*: the nominate variety, occurring from Newfoundland west to Lake Superior and south along the Atlantic coast to South Carolina, *J. pelocarpus* var. β *crassicaudex* Engelm. from Florida, and *J. pelocarpus* var. γ *subtilis* (E. Meyer) Engelm. from Canada. *Juncus pelocarpus* var. *crassicaudex* had previously been described by Chapman (1860) as a separate species, *J. abortivus*, similar to *J. pelocarpus* but more robust, with a thicker rhizome. Likewise, *J. pelocarpus* var. *subtilis* was originally described by Meyer (1823) as *Juncus subtilis*, a species with creeping or floating stems, proliferations arising from the nodes, and the inflorescence much reduced (often two-flowered).

Since Engelmann's revision, two other infraspecific taxa of *Juncus pelocarpus* have been named. St. John (1921) described a diminutive variant from Sable Island, Nova Scotia, as *J. pelocarpus* var. *sabulonensis*. He reported it to be nonbulbiferous with curving, prostrate or depressed culms 2–6 cm high, flowers crowded on the inflorescence, and capsules 2.5–3.5 mm long, while the nominate variety had longer straight culms, diffuse inflorescences, and capsules 3–4 mm long. Fassett (1930) described a sterile, submersed form with flaccid, incompletely septate leaves from northern Wisconsin as *J. pelocarpus* f. *submersus*.

Fernald (1950) accepted St. John's and Fassett's taxa, and treated Engelmann's three varieties instead as distinct species. He redefined *J. abortivus* to include plants from South Carolina to southeastern Virginia as well as from Florida, with *J. pelocarpus* extending southward only as far as Delaware. He also provided additional distinguishing characters: *J. abortivus* was reported to differ from *J. pelocarpus* in its acute rather than obtuse sepals, and a cyme $\frac{1}{6}$ – $\frac{1}{2}$ the length of the stiffly erect culm rather than $\frac{1}{3}$ – $\frac{2}{3}$ the length of the ascending slender culm; *Juncus subtilis* was reported to have anthers and filaments approximately equal in length, rather than the anthers greatly exceeding the filaments in length as in *J. pelocarpus* and *J. abortivus*. Most recent floristic works (e.g., Radford et al. 1968; Scoggan 1978; Godfrey & Wooten 1979; Coile & Jones 1985; Clewell 1985) have also treated each of Engelmann's varieties occurring within their regions as distinct species. Gleason and Cronquist (1963), however, adopted a

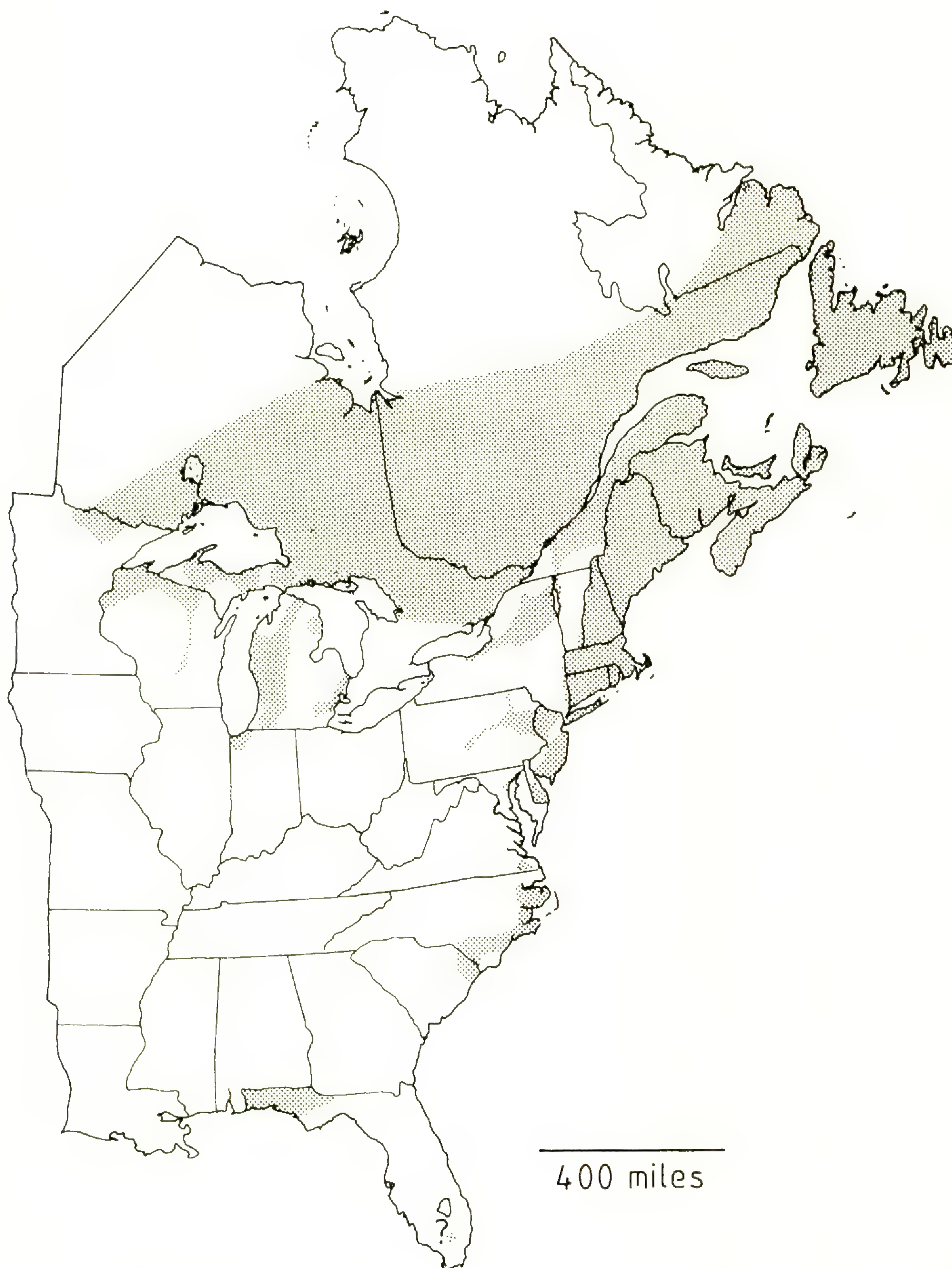


FIG. 1. Distribution of *Juncus pelocarpus* sensu Engelmann in eastern North America. Distribution based on herbarium material and literature reports from Deam (1940), Lakela (1965), McIntosh (1950), Ogden (1974), Radford et al. (1968), Scoggan (1978), Seymour (1969), Stone (1912), Tatnall (1946), Voss (1972), and Wherry et al. (1979). We were unable to locate specimens to substantiate presence of the species in the Piedmont and Coastal Plain of Georgia, whence it was reported by Duncan and Kartesz (1981). We regard as suspect the locality marked by "?" in southern Florida; it is based on a single specimen purportedly collected from an area in which suitable habitat is unlikely to be present.

treatment intermediate between Engelmann's and Fernald's, and accepted *Juncus subtilis* as a distinct species while retaining *J. abortivus* as *J. pelocarpus* var. *crassicaudex*.

We became aware of this diversity of taxonomic opinion in the course of ecological studies of *Juncus pelocarpus* in northern Michigan, where the typical and submersed forms occurred together, and conducted a study to determine which, if any, of past taxonomic treatments was most appropriate. As *Juncus subtilis* is poorly represented in herbarium collections and we did not have the opportunity to observe it in the field or greenhouse, we have, for the present, accepted the consensus of recent opinion and exclude it from further consideration here. We present an evaluation of the remainder of the taxa included in *Juncus pelocarpus* s.l., and propose a treatment of the group.

METHODS

We examined plants in the field in Michigan at Bodi Lake, Luce County, and Vincent Lake, Cheboygan County, in 1981, and near Orangeville, Barry County, in 1986; in New Jersey in Forked River, Ocean County, and near Chatsworth and Greenbank, Burlington County, in 1983; and in Virginia in City of Suffolk County in 1983. At all localities we made notes concerning the habitat and collected living plants. Field-collected plants grown in a greenhouse at the Matthaei Botanical Gardens, University of Michigan, produced bulbils that were sown in pans of well-watered standard potting soil in early 1984. These bulbil-grown plants were harvested at the end of the growing season and pressed; measurements of cultivated material were taken from the pressed specimens. Voucher specimens are deposited at MICH. These specimens, along with our field collections and herbarium specimens from DAO, GA, GH, MICH, MSC, and NCU, were used in comparison of the different taxa. Measurements of rhizomes, culms, and capsules were made on dried specimens, while perianth parts were soaked before being examined and measured.

Seed morphology has traditionally been important in *Juncus* systematics, although it had not been previously used to separate taxa in this group. Recently, examination of *Juncus* seeds with the scanning electron microscope has revealed important new characters (Brooks & Kuhn 1986; Ertter 1986). We therefore examined surface morphology of mature seeds from ten populations representing recognized taxa and the entire ranges of the taxa: Florida, *Godfrey & Houk 61553* (NCU); Indiana, *Umbach 6310* (MICH); Massachusetts, *Fernald & Long 18213* (GH); Michigan, *Murray s.n.* (MICH); Minnesota, *Lakela 16951* (DAO); New Jersey, *Hermann 3656* (GH); North Carolina, *Bell 16039* (NCU); Nova Scotia (Sable Island), *Catling 2066* (MICH); Quebec, *Victorin & Germain 264* (DAO); and Virginia, *Fernald & Long 12611* (GA). The seeds were gold-coated and examined and photographed at 150 $\times$ and 680 $\times$ using a JEOL JSM-U3 scanning electron microscope.

At the Vincent Lake locality in the northern lower peninsula of Michigan, reciprocal transplants of emerged and submersed forms were made in summer 1981. Two replicate 15 cm $\times$ 15 cm plots of the underwater form were brought to the shoreline on 1 July, 15 July, and 2 August. Two emerged and two submersed control plots were marked on 1 July, and two emerged flowering plots were transplanted to a depth of ca. 30 cm in early August. All plots were observed until 20 September.

RESULTS

Specimens from all populations had short- to long-creeping rhizomes giving rise to upright flowering culms. Rhizomes varied in diameter from 0.4 to 2.9 mm, with rhizome diameter generally increasing with decreasing latitude. Rhizomes of cultivated plants were slightly smaller than those of field specimens from the same locality (Fig. 2). Small rhizomes were whitish and thin-tissued, while larger ones were straw-colored and fibrous to somewhat woody.

Flowering culms were 5.0–69.2 cm high, usually with 1 or 2 basal leaves and 1–4 cauline leaves, each consisting of a sheathing portion 9–23 mm long with membranous auricles on either side at the apex, and a terete septate blade equalling or up to six times as long as the sheath. The blade of the basal leaf was sometimes reduced to a 1–2 mm long mucro; this condition was most frequent in southeastern specimens but was observed in specimens from throughout the range. Culms and leaves were often red-tinged both in live plants and in dried specimens. At the Barry County, Michigan, locality, new rhizomes were observed sprouting from the nodes of submersed flowering culms from the previous growing season.

The inflorescence consisted of 2–7 diverging primary branches subtended by a bract resembling a small culm leaf. Inflorescences were 2.1–25.0 cm in height, whereas the vegetative portion of the culm was 2.9–54.6 cm in height; the size of both again generally increased from north to south (Fig. 3, 4). The inflorescence

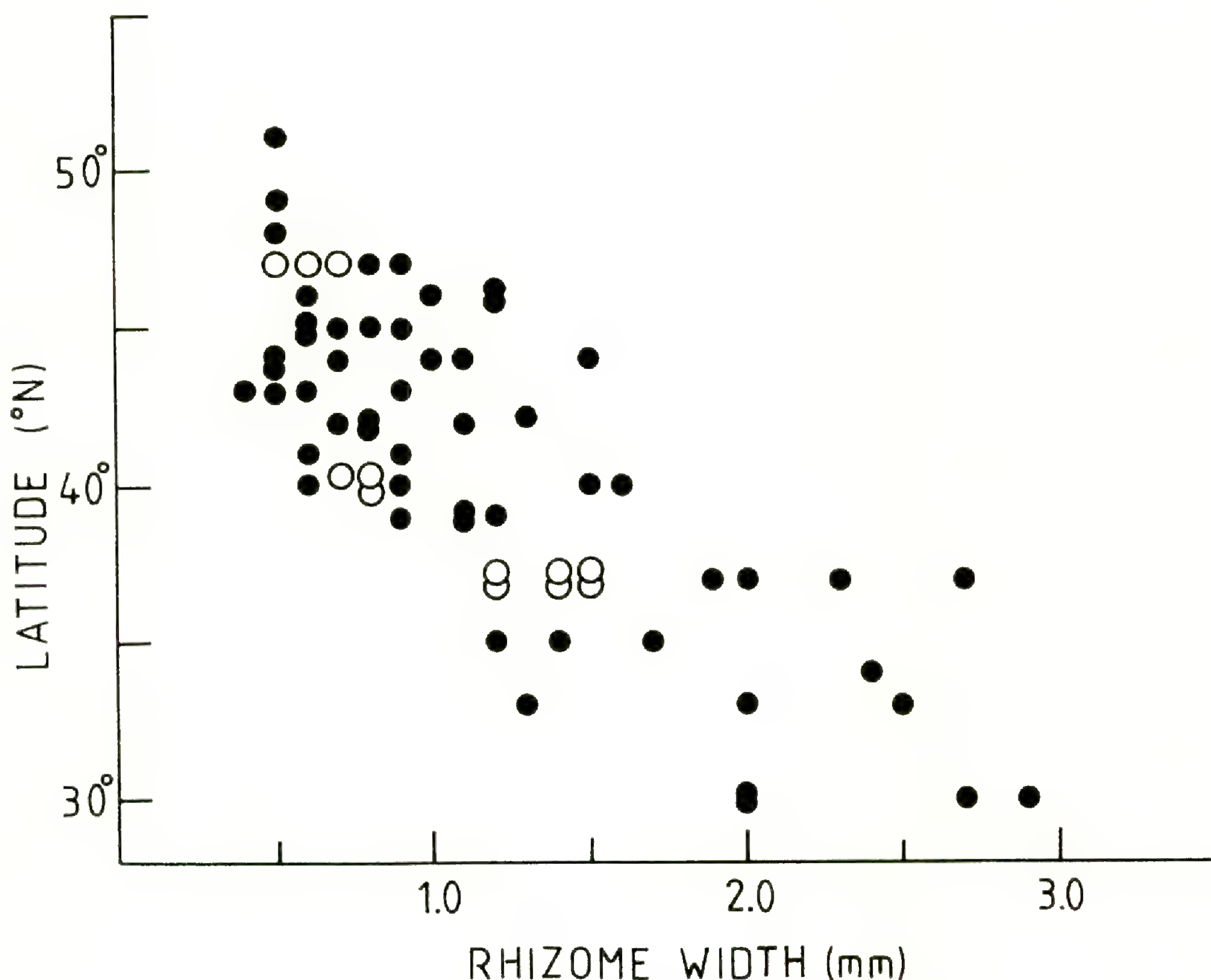


FIG. 2. Plot of rhizome width versus latitude for *Juncus pelocarpus* sensu Gleason and Cronquist. Open circles represent measurements from cultivated plants.

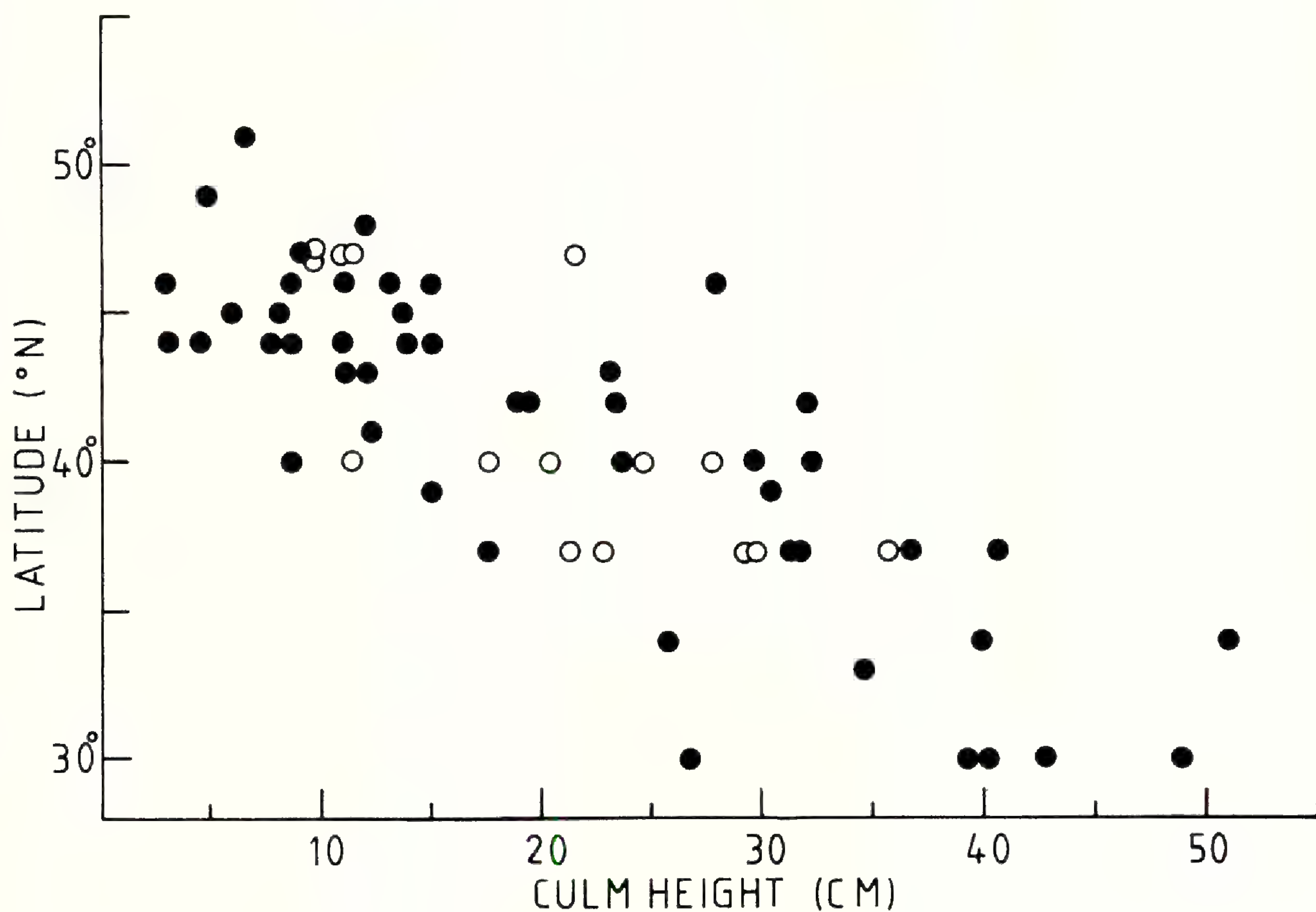


FIG. 3. Height of vegetative portion of culm versus latitude for *Juncus pelocarpus* sensu Gleason and Cronquist. Open circles represent measurements from cultivated plants.

formed 15–49% of the total height of the flowering culm, with a range of 23–48% for specimens north of 38°N, and 15–49% for specimens south of 38°N. The proportion of flowers to bulbils produced within an inflorescence varied widely within populations studied. Environmental factors including shading, submersion, and early or late inflorescence initiation all increased the proportion of bulbils produced (unpublished data). Bulbils were present, although few, in the paratype material of *Juncus pelocarpus* var. *sabulonensis* (Macoun 22631) and occur more abundantly in later collections of *sabulonensis*-like material.

Sepals of all specimens examined were about 2 mm long, navicular, with involution of the hyaline margin most produced toward the apex and more pronounced the greater the width of the hyaline tissue relative to the thickened medial portion of the sepal. The shape of the sepal apex often cannot be seen in abaxial view if it is rolled inward. The thickened medial portion may or may not reach the apex of the sepal; this may vary within the same specimen. No difference was observed in sepal morphology between recognized taxa or geographically defined groups.

Capsules were 2.5–3.0 mm long in *Juncus pelocarpus* var. *sabulonensis* specimens, and otherwise 2.0–3.5 mm long. Capsules were fusiform in shape, acute to subulate at the apex, and terete or less frequently slightly three-angled in cross section.

The seeds were ovoid in shape, with a conspicuous pattern of longitudinal and latitudinal markings. Longitudinal straight and crenulate ridges run the entire length of the seed, with transverse connecting ridges at regular intervals. These lines form a checkered pattern on the seed surface (Fig. 5a, c, e). At higher

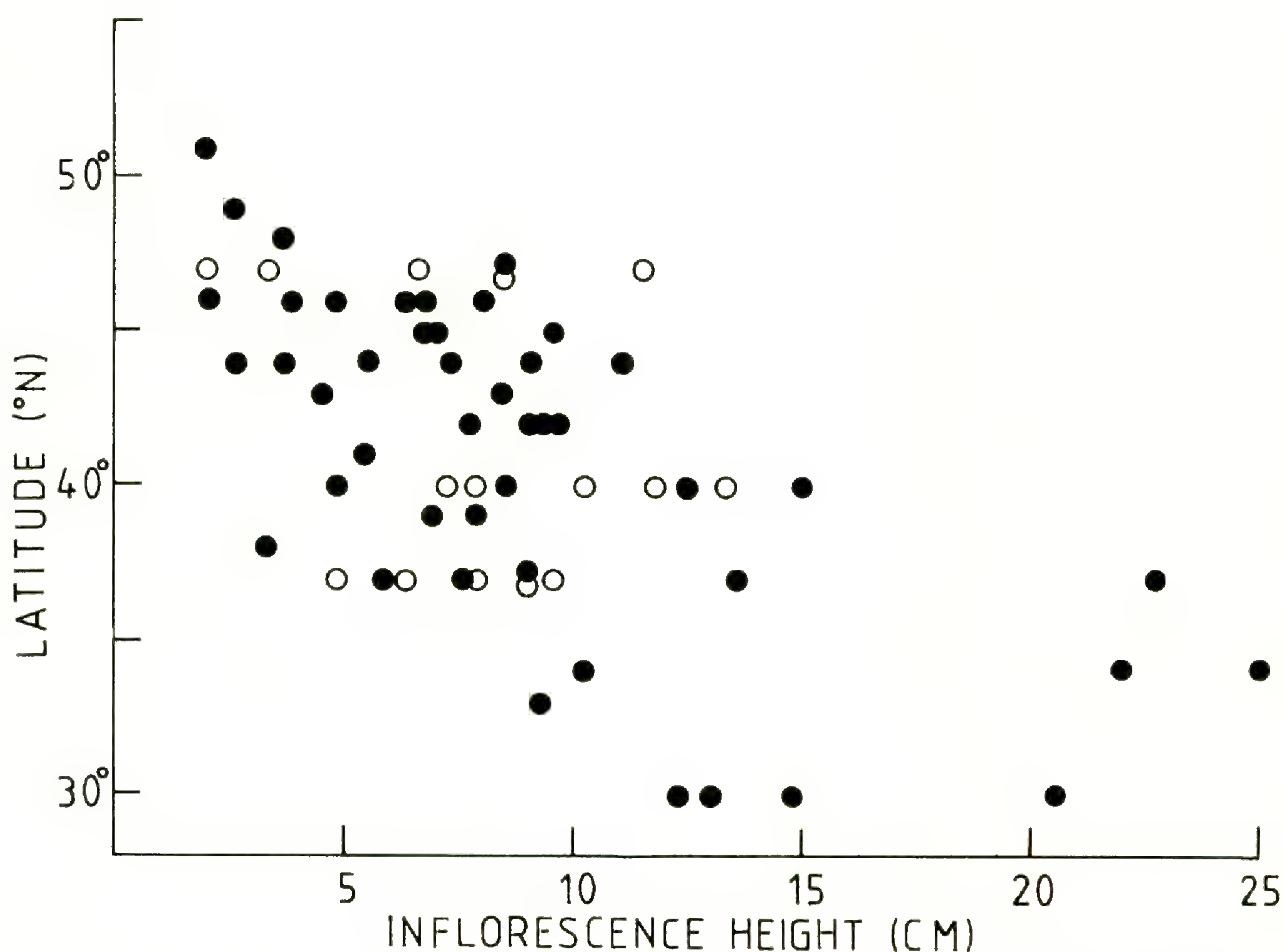


FIG. 4. Height of inflorescence versus latitude for *Juncus pelocarpus* sensu Gleason and Cronquist. Open circles represent measurements from cultivated plants.

magnification a cobwebby or marbled sculpture is visible on the surface between the ridges (Fig. 5b, d, f). No consistent pattern of variation was found among the samples.

Submersed plants transplanted to the shoreline produced flowering culms and stiff reddish leaves within 9–12 days of transplanting in all trials. Conversely, emersed plants transplanted to 30 cm under water ceased producing flowering culms after transplanting, with existing flowering culms turning brown at the tips and setting no fruit. Bulbils already present on these inflorescences continued to grow underwater. New leaves produced by these submersed plants were flaccid and lacked red pigment. Neither set of controls underwent such transformations during the study period.

DISCUSSION

Our data do not support taxonomic recognition of *Juncus pelocarpus* f. *submersus*, as a given individual of this taxon can be readily interconverted into the typical form through environmental manipulation. The underwater morph is not sterile; the cue for inflorescence initiation is simply not transmitted through water. The difference in plant form is one of heterophylly, a common feature of aquatic plant morphology.

Juncus pelocarpus var. *sabulonensis* cannot be consistently separated from the nominate variety; its retention as a taxonomic entity thus seems unwarranted.

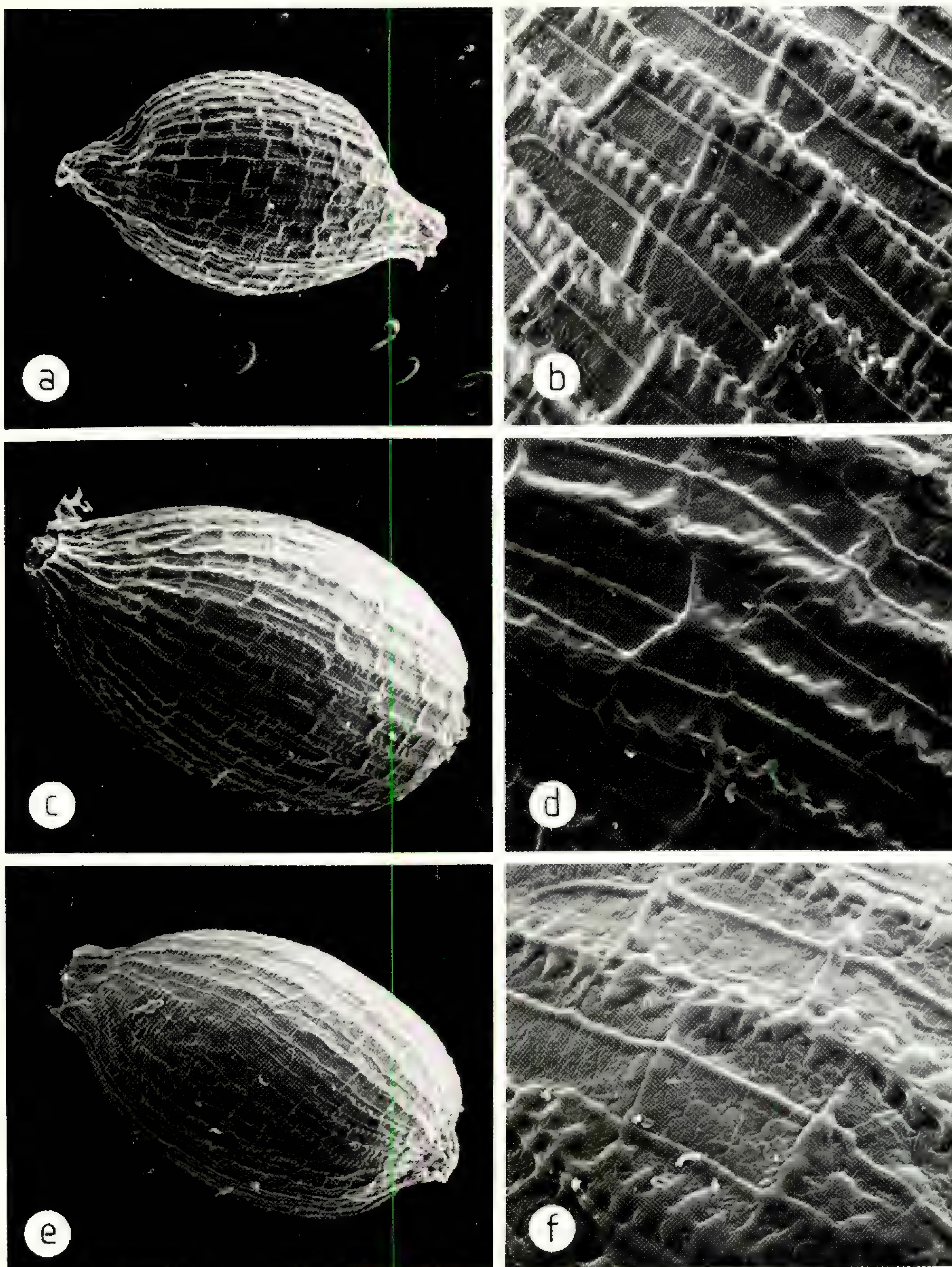


FIG. 5. Scanning electron micrographs of seed surface morphology of *Juncus pelocarpus*. a, b. *Murray s.n.* from Michigan. c, d. *Catling 2066* from Sable Island, Nova Scotia. e, f. *Godfrey 61553* from Florida. Whole seeds $\times 110$, closeups $\times 504$.

Capsule and culm size are well within the range of *Juncus pelocarpus* var. *pelocarpus*. The depressed culms and crowded inflorescences noted by St. John in the type material grade into the nominate variety in other collections and in our experience are common in plants growing on exposed, relatively dry sites. Mate-

rial of *J. pelocarpus* var. *sabulonensis* examined by St. John is indeed bulbiferous, contrary to his description.

Juncus specimens from the southeastern United States examined in our study generally have stouter rhizomes, and taller vegetative portions of the culm and inflorescences than those from more northern localities. The ratio of inflorescence height to total plant height, used by Gleason and Cronquist (1963) and Fernald (1950) to distinguish the northern from the southern plants, had a larger range of values for the southern plants (15–49%) than for the northern (23–48%) plants. The more robust habit of the southern plants is maintained under common-garden conditions. However, the increases in rhizome diameter, height of vegetative portion of the culm, and height of inflorescence are all gradual, and continue trends already occurring in plants from farther north (Figs. 2, 3, 4). In other characters we found no difference between northern and southern plants; leaf morphology and seed surface ornamentation were indistinguishable, and sepal shape appeared more variable within an individual specimen than between specimens from the extremes of the range.

We conclude that the evidence favors treating the northern and southern populations as conspecific. This treatment, we believe, places proper emphasis on common life history features of the two populations, such as the bulbiferous inflorescences and occurrence in soft-water habitats, as well as on their homogeneity in qualitative morphological details, such as the diffuse inflorescences, seed ornamentation, and sepal shape. It is appropriate, however, to distinguish the geographically isolated southeastern plants, with their larger rhizomes and generally more robust habit, from the nominate variety: *Juncus pelocarpus* var. *crassicaudex* (= *J. abortivus*) occurring from 37°N southward, and *J. pelocarpus* var. *pelocarpus* occurring from 39°N northward.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance of L. Thomson, D. Eggers Ware, T. Wieboldt, A. A. Reznicek, R. Rabeler, the staff of Matthaei Botanical Gardens, especially M. Hommel, and the curators of the herbaria cited in the text.

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SABAH FERNS COLLECTED BY JOHN H. BEAMAN

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The following notes are based in large part on new collections from Borneo, the heart of the vast botanical paradise that is Malesia. The southern portion of Borneo, with about 73% of the island's total land area of over 467,000 km², is now Kalimantan in Indonesia, and the remainder is divided into the small nation of Brunei and the two states of East Malaysia, Sarawak and Sabah. Previously called British North Borneo, Sabah is the source of recent expertly made botanical collections by Dr. John H. Beaman of Michigan State University (MSC).

From June 1983 to August 1984 Beaman collected about 4100 numbers of plants, of which 231 are ferns representing 129 species. Nearly all his ferns were obtained in the Crocker Range, which extends from northeastern Sarawak to northern Sabah and dominates the western portion of the latter. The Crocker Range is highlighted by the magnificent Mt. Kinabalu, at 4101 m the highest in Southeast Asia and Malesia outside the central range in New Guinea, and the subject of a delightful volume issued by the Sabah Society (1978). Unfortunately, the precious biota of Mt. Kinabalu is not being adequately protected (Bailes 1985). Because the summit area and upper elevations of Mt. Kinabalu are relatively well-known botanically, Beaman focused his efforts on low and middle elevation forests and gave special attention to the flora on soils derived from ultramafic (mostly serpentine) rocks.

Because of chemical and physical peculiarities, serpentine areas often have a characteristic scrubby vegetation, including some species that seem to be totally restricted to that substrate. Kruckeberg (1964) reviewed ferns (all north temperate) reported as serpentinophilic to varying degree. The most consistent of the reports refer to a European *Asplenium* once named *A. serpentini* Tausch (now *A. cuneifolium* Viv.) and to several North American taxa in *Polystichum*, *Adiantum*, and *Cheilanthes* (*Aspidotis*). Of 609 Jamaican pteridophytes, Proctor (1985, p. 452) noted only one *Polystichum* as confined to serpentine. The precise factors determining affinity to serpentine may not be the same in all cases. Smith (1975), experimenting with *Aspidotis*, discovered that spore germination and gametophytic requirements were not correlated with edaphic preference, which leads to the conclusion that sporophytic needs must be crucial. This may be a high selenium requirement as suggested by Lellinger (1985, pp. 149, 278).

Among the Beaman fern collections, 66 (representing 48 species) were on ultramafic terrain. Eight of his 20 collections discussed in this paper, including six terrestrial and one epiphytic species, were from this type of substrate. Thus it would appear that a disproportionately large percentage of the most significant Beaman fern collections are terrestrial species from ultramafic habitats.

By far the most important reference for Sabah ferns is Christensen and Holttum's *The Ferns of Mount Kinabalu* (1934) in which earlier literature is cited, and which also contains information about the botanical history and fern ecology of

the mountain. Their 417 species do not include those of the surrounding lowlands or the number would have been considerably augmented. Copeland's *Additional Ferns of Kinabalu* (1935) raised the tabulation to 437, and a recent estimate of species known from within only the official boundaries of Kinabalu Park (formerly Kinabalu National Park) is 450 (Holttum 1978). In a study of the pteridophytes of nearby Gunung Mulu in Sarawak, Parris et al. (1984) estimated that only one-third of the 71,000 hectares of Kinabalu Park had been scientifically explored, a figure corroborated by Beaman (pers. comm.), so it is expected that the number of recorded species will continue to increase. This extreme richness in ferns of this single mountain, with perhaps 500 species, may be appreciated by comparing it with the total of 317 species (Lellinger 1985) for the United States and Canada.

Other essential literature for Sabah ferns includes the ongoing revisions for *Flora Malesiana*. Those already published are Gleicheniaceae and Schizaeaceae (Holttum 1959), Cyatheaceae (Holttum 1963), excerpted for Borneo, and including seven tree fern species known only from Kinabalu (Holttum 1974), Lindsaea Group (Kramer 1971), Lomariopsis Group (Holttum & Hennipman 1978) and Thelypteridaceae (Holttum 1982). The phytogeography of some primitive ferns of Mt. Kinabalu was the subject of another paper by Holttum (1964). Tagawa (1974–75) enumerated pteridophytes collected in Sabah by a Japanese expedition in 1968–69. Also relevant are thirteen recent papers by Iwatsuki et al. (1965–84) about pteridophytes of other parts of Borneo.

Instead of listing all the ferns collected by Beaman, I am detailing only those that are especially noteworthy for one reason or another, such as being new records, second collections, or of nomenclatural or geographical interest; also included are a few other notes from specimens of other collectors at MICH. All are arranged in alphabetical order by accepted name. *Adiantum opacum* and *Tectaria balabacensis*, both new records for Borneo, are here first suggested as probable serpentinophiles; other possible candidates are *Adiantum hosei*, *Ctenitis atrorubens*, and *Diplazium beamanii*. A complete set of Beaman's Sabah ferns has been deposited in the University of Michigan Herbarium (MICH).

Acrophorus nodosus Presl, Tent. Pterid. 94, t. 3, f. 2. 1836. *Aspidium nodosum* Bl., Enum. Pl. Jav. 2: 171. 1828, non Willd., 1810. *Acrophorus blumei* Ching ex C. Chr. & Holtt., Gard. Bull. S. S. 7: 226. 1934, nom. superfl.

The earliest description of a species of *Acrophorus* was published by Blume who chose a name previously used by Willdenow. When Presl established *Acrophorus* in 1836, he provided a new name for Blume's species; this is the first valid name available in the genus. The later *A. blumei* is superfluous.

All specimens of *Acrophorus* I have seen from Borneo, the Philippines, and Java have round-reniform dryopteroid indusia, whereas many from elsewhere in Asia have very small convex cystopteroid indusia. Five new species from China were described by Ching & Wu in Wu, Acta Phytotax. Sinica 21: 379–383. 1983, and an unpublished new species in Sarawak is listed by Parris et al. (1984, p. 223). *Acrophorus* is closely allied to *Diacalpe*, *Peranema*, *Stenolepia*, *Nothoperanema*, and *Dryopsis*, the last only recently described by Holttum & Edwards, Kew Bull. 41: 171–204. 1986.

SABAH SPECIMEN (additional to those cited by Christensen & Holttum, 1934): *Beaman* 8028, Tambunan Dist., Crocker Range, 1700–1800 m, terr. in oak-laurel forest, 5°49'N, 116°20'E.

Adiantum hosei Baker, J. Bot. 26: 324. 1888; Tagawa, Acta Phytotax. Geobot. 26: 167. 1975.

A. scabripes Copel., Philip. J. Sci. 7C: 55, pl. 5. 1912; Fern Fl. Philip. 1: 164. 1958.

In this species the acroscopic ends of the lower epidermal cells between veins tend to curl up from the surface and become almost hairlike, resulting in the very rough texture indicated by Copeland's epithet.

Adiantum hosei was originally described from Sarawak and *A. scabripes* from Mindanao. The discovery of the species in Sabah, which is intermediate, was to be expected and was already recorded by Tagawa, who was, however, unaware of the Philippine occurrence. *Adiantum scabripes* is here considered for the first time a synonym of *A. hosei*. In Index Filicum Suppl. 3: 19. 1934, Christensen reduced *A. scabripes* to *A. monosorum* Bak. of the Solomons but retreated from that decision in Dansk Bot. Arkiv 9(3): 54. 1937.

Despite one record from limestone (*Brooks s.n.*, Feb. 1907, Sarawak, Bidi), the distribution of this species leaves open the possibility that it has serpentophilic tendencies.

SABAH SPECIMENS: *Beaman 10302*, Labuk & Sugut Dist., near Karamuak R., 100 m, ultramafic geology, 5°31'N, 117°03'E; *Clemens 30841*, Kinabalu, Penibukan, in canyon, 4000 ft.

Adiantum opacum Copel., Philip. J. Sci. 1 Suppl. 255, pl. 3. 1906; Fern Fl. Philip. 1: 163. 1958.

A. cupreum Copel., Leaf. Philip. Bot. 4: 1152. 1911; Fern Fl. Philip. 1: 163. 1958.

Adiantum opacum described from Palawan and *A. cupreum* from Sibuyan were believed to be Philippine endemics by Copeland; I consider them one species, here first reported from Borneo. Distinguishing characters are the deciduous pinnules and the rachis with stiff hairs above. Because all five collections of this species (four from Palawan) are from ultramafic areas, according to geological information from Hamilton (1979) and the Philippine Bureau of Mines "Geological Map of the Philippines," 1963, and because the species is relatively rare, I believe it to be a true serpentophile.

SABAH SPECIMEN: *Beaman 9054*, Ranau Dist., ultramafic slopes and cliffs on SW side of Lohan R., 750–950 m, 6°00'N, 116°41'E.

Asplenium klossii C. Chr., Gard. Bull. S. S. 7: 278, pl. 60. 1934; Tagawa, Acta Phytotax. Geobot. 27: 139. 1976.

Asplenium klossii is a close relative of *A. tenerum* Forst. but is reliably distinguished by the non-auriculate, cordate-based, subopposite pinnae and the narrow, caudate frond apex. The original description was based on a single collection made near Sandakan. The species was also later reported from near Tawau in southeastern Sabah by Tagawa and thus is apparently endemic to eastern Sabah. Beaman's collection is larger than that described by Christensen, with fronds to 57 × 14 cm bearing up to 13 pairs of pinnae, the largest 8.5 × 1.4 cm.

SABAH SPECIMEN: *Beaman 10198*, near Tawau, epiphytic, 100–120 m, 4°24'N, 117°53'E.

Asplenium lobulatum Mett. ex Kuhn, Linnaea 36: 100. 1869. SYNTYPES: Hawaii, Remy, Gaudichaud, Meyen (n.v.).

A. steerei Harr., J. Linn. Soc. Bot. 16: 28. 1877; Copeland, Fern Fl. Philip. 3:

438. 1961; Price, Contr. Univ. Michigan Herb. 15: 200. 1982; Parris et al., Pterid. G. Mulu Nat. Park 215. 1984. LECTOTYPE: Philippines, Luzon, *Steere s.n.* (MICH).
- A. pseudofalcatum* Hillebr., Fl. Haw. Is. 597. 1888. SYNTYPES: Hawaii, specimens from five localities (n.v.).
- A. pseudofalcatum* var. *obtusum* Hillebr., Fl. Haw. Is. 598. 1888. SYNTYPES: specimens from three localities (n.v.).
- A. cuneatiforme* Christ, Bull. Herb. Boiss. II, 4: 613. 1904; DeVol & Kuo, Fl. Taiwan 1: 481. 1975. TYPE: China, Taiwan, *Faurie 661* (n.v.).
- A. laxivenum* Copel., Philip. J. Sci. 2C: 132. 1907. TYPE: Philippines, Mindoro, *Merrill 5892* (holotype lost at PNH in 1945; lectotype, here designated: MICH; isoelectotype: US).
- A. cromwellianum* Rosenst., Fedde's Repert. 10: 327. 1912; Nakaike, Bull. Natn. Sci. Mus. Tokyo ser. B, 9: 95. 1983. TYPE: New Guinea, *Bamler K19* (n.v.).
- A. pseudofalcatum* var. *subintegrum* Rosenst., Hedwigia 56: 334. 1915 ('*subintegra*'). TYPE: China, Taiwan, *Faurie 455* (isotype: MICH).
- A. pseudofalcatum* var. *subintegrum* f. *obtusatum* Rosenst., Hedwigia 56: 334. 1915 ('*obtusata*'); *A. arisanense* Tag., J. Jap. Bot. 14: 707. 1938. TYPE: China, Taiwan, *Faurie 455 bis* (n.v.).
- A. benguetense* Hieron., Hedwigia 60: 264. 1919; Price, Kalikasan 2: 112. 1974. TYPE: Philippines, Luzon, *Elmer 6012* (isotype: MICH).
- A. ledermannii* Hieron., Bot. Jahrb. 56: 150. 1920. SYNTYPES: New Guinea, *Ledermann 10064, 11059, 11066, 12457* (n.v.).
- A. loxocarpum* Copel., Univ. Calif. Publ. Bot. 14: 375, t. 59. 1929. TYPE: Sumatra, *Bartlett 6605* (holotype: UC; isotype: MICH).
- A. acutiusculum* auct. non Bl.: Racib., Pterid. Fl. Buitenz. 217. 1898; C. Chr. & Holtt., Gard. Bull. S. S. 7: 280. 1934, p.p.; Backer & Posth., Varenfl. Java 140. 1939; Tagawa, Acta Phytotax. Geobot. 27: 140. 1976; Iwatsuki & Kato, Acta Phytotax. Geobot. 31: 168. 1980.
- A. insiticism* auct. non Brack.: Brownlie, Pterid. Fl. Fiji 222. 1977.

This clearly marked species is distributed from Taiwan to Sumatra, then east to New Ireland (*Croft LAE 65283*), New Caledonia (*Franc 334*, MICH, 3 sheets), Fiji, and Hawaii. In Hawaii, the source of the syntype collections, the variability of the species is greatest and encompasses almost all pinna-shapes and degree of dissection developed elsewhere. In Java, as in Borneo, the species was incorrectly called *A. acutiusculum* Bl., a name now known to be a synonym of *A. longissimum* Bl. (Price 1982).

Another frequent misidentification is as *A. insiticism* Brack., U. S. Expl. Exped. 16: 161. 1854; Atlas t. 22. 1855. By courtesy of Dr. D. B. Lellinger of the U.S. National Herbarium, I was able to examine Brackenridge's holotype, sheet *US 50453*, collected "in forest, return from Mauna Kea, Hawaii." The specimen is not proliferous, although wrongly described and drawn as such, but otherwise precisely matches the plate. I identify it as a large elaborate form of the non-proliferous *A. contiguum* Kaulf., not a close relative of *A. lobulatum*.

Distinguishing characters of *A. lobulatum* are: rhizome short; fronds pinnate to bipinnate, pinnae subentire to coarsely toothed; lamina texture chartaceous, often gemmiferous along rachis near apex; costae slender and raised above; veins

widely spaced, often 2 mm apart, teeth bluntly pointed, spaced as veins; sori all equally divergent from costa; usually epiphytic at high elevations.

SABAH SPECIMENS: *Clemens* 33140, *Topping* 1814, both from Mt. Kinabalu.

Colysis loxogrammoides (Copel.) Price, comb. nov. *Polypodium loxogrammoides* Copel., Philip. J. Sci. 7C: 65. 1912. TYPE: Sarawak, Limbang, *Sar. Mus. Coll. no. 17, 1910* (MICH).

Polypodium polysorum Brause, Bot. Jahrb. 56: 203. 1920; C. Chr. & Holtt., Gard. Bull. S. S. 7: 308. 1934; *C. polysora* (Brause) Copel., Gen. Fil. 199. 1947. Brause cited four Ledermann syntypes from New Guinea.

Colysis loxogrammoides is a relative of *C. macrophylla* (Bl.) Presl and is distinguished by the scandent, thick, woody rhizome with long, wiry clasping roots; paleae pale brownish-grey, subclathrate with cloudy luminae, margins erose-denticulate; lamina not or only slightly dimorphic, apex long caudate-acuminate; sori with broad receptacles, strong, thick, uninterrupted. An additional synonym may be *Pleopeltis pseudoloxogramma* v. A. v. R., Bull. Jard. Bot. Buitenz. III, 5: 218, fig. b, c. 1922; *Polypodium pseudoloxogramma* (v. A. v. R.) C. Chr., Ind. Fil. Suppl. 3: 156. 1934; *Selliguea pseudoloxogramma* (v. A. v. R.) Ching, Sunyatsenia 5: 260. 1940, although the type from Ceram, *Kornassi 1373* (n.v.), was described by Alderwerelt as having entire paleae.

SABAH SPECIMENS: *Clemens* 26184 (BO, K, MICH), 28642 (K, MICH); *Topping* 1572 (MICH); *Shim Phyu Soon SAN 81676* (K). Also, from Sarawak, G. Mulu Natl. Park, *I. Nielsen 637* (AAU, photocopy kindly sent from K by Dr. B. S. Parris).

Ctenitis atrorubens Holtt., Blumea 31: 29. 1985.

This recently recognized species from the Philippines was represented by only the single specimen at MICH until Beaman's collection confirmed its distinctness, constancy, and continued existence. It may be a serpentinophile although two collections are not a sufficient sample.

SABAH SPECIMEN: *Beaman 10734*, Ranau Dist., Pinosuk Plateau, ca. 8 km ESE of Desa Dairy, 1380 m, ultramafic soil, logged forest, 6°01'N, 116°37'E.

Dicranopteris clemensiae Holtt., Reinwardtia 4: 275. 1957; Fl. Males. II, 1: 32, fig. 14b–c. 1959.

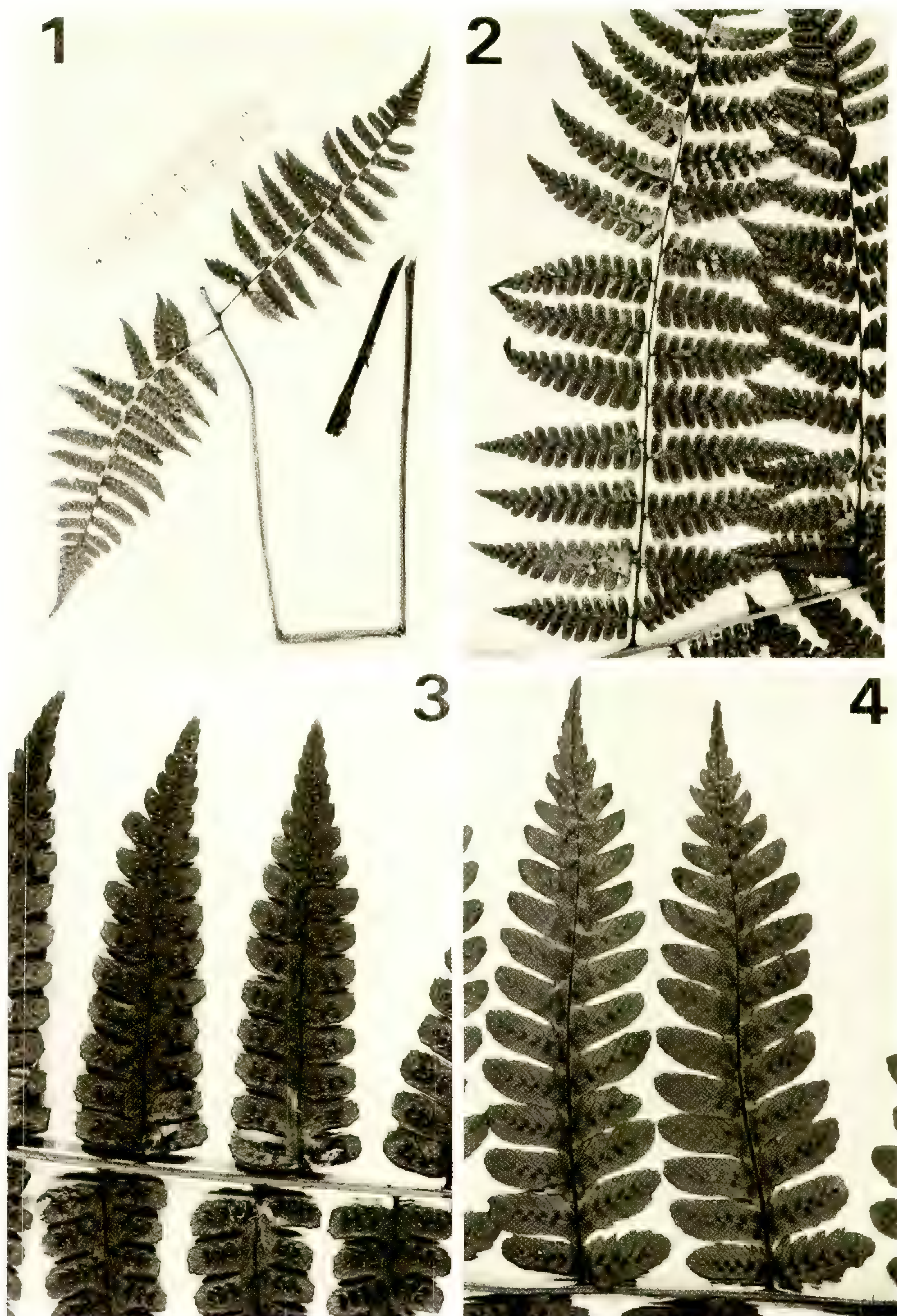
Beaman's gathering is only the second collection, and agrees well in all respects with Holttum's description although the spores were gone. Monolete spores as found in this species are unusual in Gleicheniaceae. Clemens's Kinabalu type collection was made at approximately the same elevation as Beaman's.

SABAH SPECIMEN: *Beaman 8020*, Tambunan Dist., Crocker Range, SW side of ridge in oak-laurel forest, 1700 m, 5°49'N, 116°20'E.

Diplazium beamanii Price, sp. nov.

Figs. 1–3.

Caudex erectus 3 dm altus. Paleae ad bases stipitum castaneae concolorae integrae ovatae usque 10 × 4.5 mm. Lamina ovata, ad basim profunde tripinnatifida; pinnae usque 37 cm longae; pinnulae usque 8 × 2 cm; segmenta subtruncata leviter denticulati-crenulata sinibus angustis separata. Sori 1.0–2.5 mm longi, cos-



FIGS. 1-4. *Diplazium*. 1-3, *D. beamanii*, type collection. 1. Stipe and basal pinnae, $\times 0.2$. 2. Middle pinnae, $\times 0.3$. 3. Pinnules, $\times 0.9$. 4. *D. mollifrons*, isotype (Elmer 22375, MICH); pinnules, $\times 0.9$.

tales vel costulares. Indusia 0.8 mm lata, primo allantoidea, post apertione supra pallide brunnea super soros arcuata, ad marginem erosa, infra hyalina ad laminam appressa. Sporae dilute brunneae sublaeves.

Caudex erect, forming a trunk 3 dm high. Paleae at stipe base castaneous, concolorous, entire, ovate, to 10×4.5 mm. Stipes stramineous, 66 cm long, 7 mm thick at base, sparsely muricate. Lamina ovate, 60 cm long, bipinnate plus deeply pinnatifid at base, rachises strongly papillose within at junctions. Pinnae lanceolate, in alternate pairs, the basal pair slightly reduced and with stalks 2.5 cm long, the subbasal largest, to 37 cm long with stalk 1 cm, basal acroscopic pinnules slightly reduced. Pinnules lanceolate, the largest shortly acuminate, stalked to 1 mm, to 8×2 cm, lobed to ca. 2 mm from costa, the pinnule-costae bearing dark brown contorted irregularly toothed paleae to 2.5×0.7 mm. Segments subtruncate with narrow sinuses, slightly denticulate-crenulate, veins to 5 pairs, usually unbranched. Sori 1.0–2.5 mm long, basal acroscopic sori of a vein-group often diplazioid (paired back-to-back), strictly costal in the pinnules and costular in the lobes. Indusia 0.8 mm wide, allantoid (sausage-shaped) at first, after breaking open along the side farthest away from the vein the upper portion pale brown, arching over sorus, margin erose and irregular, the basal portion underneath the sorus hyaline, appressed to the laminar surface. Spores pale brown, nearly smooth.

TYPE: *Beaman 10724*, Sabah, Ranau Dist., Pinosuk Plateau, ca. 8 km ESE of Desa Dairy, 1380 m, in logged forest by stream in ultramafic terrain, $6^{\circ}01'N$, $116^{\circ}37'E$, 28 July 1984 (holotype: MICH; isotypes: A, K, L, MSC, UKMS).

Diplazium beamanii is closely related to *Athyrium sylvaticum* (Bl.) Milde at least sensu C. Chr. & Holtt., Gard. Bull. S. S. 7: 268. 1934 (Sabah specimens: *Clemens 29591* & *32567 bis*), which differs by stipe-base paleae black-margined and regularly toothed, lamina segments prominently toothed, sori inframedial but not costal, indusia allantoid but uniformly brown (not hyaline below sorus) among other characters. Blume's holotype from Java (*Morton photo 674*) agrees with Clemens's specimens cited above in visible details. Unfortunately, the Javan species appears to have no valid name in *Diplazium*; I therefore provide the following name: ***Diplazium allantoideum*** Price, nom. nov.; *Allantodia sylvatica* Bl., Enum. Pl. Jav. 2: 173. 1828, non *D. sylvaticum* (Bory) Sw., Syn. Fil. 92. 1806.

Diplazium woodwardioides (Presl) Holtt. from Luzon, which appears in Copeland's Fern Fl. Philip. 3: 400. 1961, as *Athyrium sylvaticum*, has a blackish brown indusium opening back to expose a fimbriate margin, not fracturing at the top; uniformly brown stipe paleae; and is constantly smaller in size of pinnules than *D. beamanii* and *D. allantoideum*. Also related is ***Diplazium mollifrons*** (C. Chr.) Price, comb. nov. (basonym: *Athyrium mollifrons* C. Chr., Leaf. Philip. Bot. 9: 3153. 1933), which differs from the three preceding species by pale brown, black-margined, toothed paleae on costae below, $\pm$ rounded segments, indusia brown, 0.5 mm wide, edge fringed with fine hairlike processes (Fig. 4). *Athyrium mollifrons* was incorrectly placed in the synonymy of *A. ophiodontum* Copel. in Fern Fl. Philip. 3: 398. 1961; I identify the latter (Type: *Ramos BS 77188*, holotype: MICH; isotype: NY) as *D. polypodioides* Bl. Both *D. beamanii* and *D. mollifrons* are possible serpentiphiles.

Diplazium dolichosorum Copel., Philip. J. Sci. 1 Suppl. 151. 1906.

This species was described from Mindanao in the southern Philippines and

considered endemic by Copeland, Fern Fl. Philip. 3: 402. 1961. It is a very close relative of *D. dilatatum* Bl., originally from Java, but my examination of Javan specimens precisely matching Blume's type shown in *Morton photos 940 & 941* reveals the following differences.

Basal sori to 13 mm long; pinnules broadly lanceolate, abruptly narrowed near apex; main rachis muricate; indusia entire. *D. dolichosorum*.

Basal sori to 7 mm long; pinnules deltoid-lanceolate, gradually tapered to apex; main rachis nearly smooth; indusial margin fimbriate-laciniate. *D. dilatatum*.

SABAH SPECIMEN: *Beaman 10641*, Ranau Dist., road from Lohan to Mamut Copper Mine, 1000 m, in dipterocarp forest, trunk-forming, 6°01'N, 116°41'E.

Grammitis palasaba Price, nom nov. *Acrosorus nudicarpus* Zamora & Co, Nat. Appl. Sci. Bull. 32: 47, f. 4. 1980, non *Grammitis nudicarpa* Copel., 1942. TYPE: Philippines, Palawan, Mt. Mantalingahan, 1700 m, epiphytic in mossy forest, *L. L. Co 1776* (isotype: MICH).

Polypodium alternidens auct. non Ces.: C. Chr. & Holtt., Gard. Bull. S. S. 7: 299. 1934, p.p.

This species is now known from two sites about 300 km apart, the type locality in southern Palawan and Mt. Kinabalu. I have seen two Kinabalu collections, made on the same date and in the same place.

As pointed out by Zamora and Co, this species fails to fit acceptably into any of the grammitid genera as formulated by Copeland. It might be a *Xiphopteris*, but the type of that genus is not different in basic characters from *Cochlidium* (Bishop 1978), which in turn merges with *Grammitis*, as argued by Proctor (1985, p. 554). For example, the New Guinean *X. conjunctisora* (Bak.) Copel. is hardly separable from *Grammitis* as indicated by Parris (1983, p. 83). Leaving this species in *Acrosorus* is not satisfactory, because its affinities are rather with *X. alternidens* (Ces.) Copel., synonym *X. murudensis* (Copel.) Copel., of Sarawak, a smaller plant of thin texture, strongly ascending unfolded segments, and pale costal hairs, and *X. hieronymusii* (C. Chr.) Holtt. of the Malay Peninsula, also a relatively thin-textured species with pale costal hairs. *Grammitis palasaba* has deciduous, usually paired, maroon setae ca. 0.3 mm long on the costa of young fronds and a thick rigid texture. The epithet *palasaba* is a compound of Palawan and Sabah.

SABAH SPECIMENS: *Clemens 10721 & Topping 1726*, Mt. Kinabalu, Paka Cave to Lobang, 15 Nov. 1915 (the Clemenses and Topping collected together).

Hymenophyllum microchilum (Bak.) C. Chr., Mitt. Inst. Allg. Bot. Hamburg 7: 143. 1928; C. Chr. & Holtt., Gard. Bull. S. S. 7: 212. 1934; Croxall in Parris et al., Pterid. G. Mulu Nat. Park 185. 1984.

Originally described from Mt. Kinabalu, this species was included in *H. polyanthos* (Sw.) Sw. by Copeland, Philip. J. Sci. 64: 97, 101. 1937, a species he placed in *Mecodium* after dividing up *Hymenophyllum*. Beaman's specimen, however, clearly shows that the species, with its receptacle exerted (when intact) and involucre cleft less than halfway, is not only distinct from *H. polyanthos* but should not even have been considered a *Mecodium*. In Copeland's scheme of classification of Hymenophyllaceae, *H. microchilum* might be a *Meringium*; in the most recent classification, it belongs in *Hymenophyllum* subgen. *Chilodium* sect.

Pseudomecodium Iwatsuki, Acta Phytotax. Geobot. 35: 172. 1984, a placement kindly confirmed by Dr. K. Iwatsuki (in litt.).

SABAH SPECIMEN (other than cited by Christensen and Holttum, 1934): *Beaman* 8024, Tambunan Dist., Crocker Range, 1700–1800 m, 5°49'N, 116°20'E.

Lindsaea gueriniana (Gaud.) Desvaux, Prodr. 312. 1827; Kramer, Fl. Males. II, 1: 230, f. 36. 1971.

This species is here reported for the first time from Sabah; the previously recorded range encompasses the Philippines and Sulawesi east to Tahiti and also Sarawak. Substrates reported include limestone, decayed wood, and serpentine.

SABAH SPECIMEN: *Beaman* 9055, Ranau Dist., steep ultramafic slopes and cliffs on SW side of Lohan R., low stature forest, 750–950 m, 6°00'N, 116°41'E.

Microsorium mindanense (Chr.) Copel., Gen. Fil. 196. 1947; Fern Fl. Philip. 3: 486. 1961.

Previously thought to be a Philippine endemic, this species is a member of the *M. heterocarpum* group, and is distinguished by the broad, more or less nest-forming frond base, and the costa strongly raised on both sides, sharply carinate below.

SABAH SPECIMEN: *Beaman* 8820, Penampang Dist., km 41, epiphytic at 1050 m, 5°51'N, 116°17'E.

Microsorium sarawakense (Bak.) Holtt., Ferns of Malaya 175, f. 84. 1955; Iwatsuki & Kato, Acta Phytotax. Geobot. 32: 122. 1981. *Polypodium sarawakense* Bak., Bot. J. Linn. Soc. 22: 228. 1886; C. Chr. & Holtt., Gard. Bull. S. S. 7: 307. 1934.

Microsorium rizalense Copel., Philip. J. Sci. 81: 42. 1952; Fern Fl. Philip. 3: 478. 1961. TYPE: Philippines, Luzon, Rizal Prov., Mt. Lumutan, *Ramos & Edaño* BS 29648 (holotype: US; isotypes: MICH, NY).

This species is of particular taxonomic interest, because I believe it clearly unites (in agreement with Sledge, Bot. Bull. Brit. Mus. 2: 144. 1960) the two genera *Microsorium* and *Phymatodes* (a name that should be retained according to Ching, Acta Phytotax, Sinica 16(4): 32. 1978) or *Phymatosorus* (proposed to replace *Phymatodes* by Pic. Ser., Webbia 28: 457. 1973).

Microsorium sarawakense has already been known from Sumatra, Malay Peninsula, and Borneo (Sarawak, Sabah, East Kalimantan); with the reduction of *M. rizalense* its range is extended over 1000 km to the North, and a collection from Ilocos Norte Prov. (Solsona, 18°09'N, 120°56'E, *Price* 2900) provides a further substantial northern range extension.

SABAH SPECIMENS (additional to those cited by Christensen and Holttum, 1934): *Beaman* 7936, Tambunan Dist., Crocker Range, epiphyte at 1450 m, 5°47'N, 116°20'E; *Beaman* 9806, NW side of Mt. Kinabalu, 800–1000 m in dipterocarp forest, 6°11'N, 116°34'E.

Prosaptia venulosa (Bl.) Price, comb. nov. *Polypodium venulosum* Bl., Enum. Pl. Jav. 2: 128. 1828; C. Chr. & Holtt., Gard. Bull. S. S. 7: 303. 1934. *Ctenopteris venulosa* (Bl.) Kunze, Bot. Zeit. 4: 425. 1846; Copel., Fern Fl. Philip. 3: 531. 1961. *Grammitis venulosa* (Bl.) R. & A. Tryon, Rhodora 84: 129. 1982.

This is the type species of the genus *Ctenopteris* which, as I argued in Contr. Univ. Michigan Herb. 15: 202. 1982, must be reduced to *Prosaptia*; an additional

generic character is the absence of hydathodes. The correct authority for the closely related *P. obliquata* is (Bl.) Mett. rather than the new combination proposed in my 1982 paper.

SABAH SPECIMENS (not previously cited): *Clemens* 31794, 33738, 50921, all from Mt. Kinabalu.

Pycnoloma metacoelum (v. A. v. R.) C. Chr., Dansk Bot. Arkiv 6(3): 77, pl. 8, f. 3; pl. 9, f. 2; pl. 10, f. 2. 1929; Parris et al., Pterid. G. Mulu Nat. Park 194. 1984. *Drymoglossum metacoelum* v. A. v. R., Bull. Jard. Bot. Buitenz. II, 28: 21, t. 2. 1918.

Beaman's collection is the first Sabah record. This species was previously known from Kalimantan, Sarawak, and the Malay Peninsula.

SABAH SPECIMEN: *Beaman* 10658, Ranau Dist., road from Lohan to Mamut Copper Mine, epiphyte high in montane dipterocarp forest, 1100 m, 6°01'N, 116°41'E.

Pyrrosia platyphylla Hovenk., Blumea 30: 207. 1984; Monog. *Pyrrosia* 222. 1986. *Cyclophorus beddomeanus* auct. non (Gies.) C. Chr.: Merrill, Univ. Calif. Publ. Bot. 15: 12. 1929.

Pyrrosia costata auct. non (Presl) Tag. & Iwats.: Iwats. & Kato, Acta Phytotax. Geobot. 32: 121. 1981.

This recently described species is similar in general appearance to the Philippine *P. splendens* (Presl) Ching, which differs by the frond margin being revolute and thickened and the stellate laminar hairs having long acicular arms. Close to *P. splendens* is *P. princeps* (Mett.) Morton [synonym: *P. aglaophylla* (Copel.) Copel.] of New Guinea. *Pyrrosia stigmosa* (Sw.) Ching of Java, Sumatra, Malaya, etc., differs by having the costa more or less rounded below (not carinate) and the lamina rapidly contracted downwards into a well-defined stipe. *Pyrrosia costata* (Presl) Tag. & Iwats. of the eastern Himalayas has the costa broadly rounded below and the laminar stellate hairs with lanceolate arms forming only a relatively thin layer. Hair types in *Pyrrosia* were reclassified by Shing, Amer. Fern J. 73: 73–78. 1983, and elaborated upon by Hovenkamp, Monog. *Pyrrosia* 40–48. 1986, who included all the species mentioned above in the "*P. costata* group."

The type of *P. platyphylla*, *Elmer* 20659 (isotype: MICH), was collected near Tawau in southeastern Sabah, near the border with Indonesian Kalimantan. The collections of Beaman are apparently the first from the main mountain mass of Mt. Kinabalu.

ADDITIONAL SABAH SPECIMENS: *Beaman* 8364 & 9243, Ranau Dist., epiphyte in low stature forest on steep ultramafic slopes and cliffs on SW side of Lohan R., 700–900 m, 6°00'N, 116°41'E.

Selliguea kamborangana (C. Chr.) Price, comb. nov. *Polypodium kamboranganum* C. Chr., Gard. Bull. S. S. 7: 306. 1934. TYPE: Sabah, Mt. Kinabalu, Kamborangah, *Holtum* 25543 (BM, n.v.).

Christensen's statement of affinity (to *Polypodium costulatum* of Sumatra) and description of the paleae as dense, entire, lanceolate, long-acuminate, and reddish brown serve to identify his plant as very probably conspecific with two sterile collections from Palawan, Mt. Mantalingahan, *Edaño PNH* 471 & 478 (both MICH). This note thus reports a second and third collection of this rare species, its range extension from Sabah to the Philippines, and also that sterile fronds may be much larger than previously known, to 19.7×6.2 cm (described by Christensen as up to 10×2 cm).

Tectaria balabacensis (Christ) Price, *Kalikasan* 1: 37. 1972. *Ctenitis balabacensis* (Christ) Copel., *Gen. Fil.* 124. 1947; *Fern Fl. Philip.* 2: 294. 1960.

Dryopteris escriptorii v. A. v. R., *Bull. Jard. Bot. Buitenz. II*, 23: 10. 1916; Price, *Kalikasan* 2: 110. 1974.

This unusual free-veined species of *Tectaria* has not been recorded outside the Philippines, although it may not be distinct from *T. trichotoma* (Fée) Tag. of Vietnam. On the basis of information from the geological sources cited above under *Adiantum opacum*, I believe that *T. balabacensis* (Philippine distribution: Balabac, the type; Palawan, four colls.; Sibuyan, two colls.; S. Luzon, Quezon Prov., one coll.) and the extremely similar *T. mesodon* (Copel.) Price (NW Mindanao, two colls.) and *T. laxa* (Copel.) Price (Luzon, Ilocos Norte Prov., seven colls.) are probable serpentinophiles.

SABAH SPECIMEN: *Beaman* 9059, Ranau Dist., on steep ultramafic slopes and cliffs on SW side of Lohan R., 750–950 m in low stature forest, 6°00'N, 116°41'E.

Tectaria zeilanica (Houtt.) Sledge, *Kew Bull.* 27: 422. 1972. *Leptochilus zeilanicus* (Houtt.) C. Chr.; Copel., *Sarawak Mus. J.* 2: 373. 1917; Ogata, *Icon. Fil. Jap.* 1: pl. 32. 1928, ('*zeylanicus*'). *Quercifilix zeilanica* (Houtt.) Copel., *Philip. J. Sci.* 37: 409. 1928; Ching, *Icon. Fil. Sin.* 3: pl. 118. 1935; DeVol & Kuo, *Fl. Taiwan* 1: 338, pl. 120. 1975, ('*zeylanica*').

Although widely distributed in southern Asia and around the borders of the South China Sea (including Vietnam, Hainan, Guangxi, Guangdong, Hong Kong, Taiwan, and Pulau Tioman off the coast of the Malay Peninsula), this oft-illustrated species has not been reported from Borneo in recent years, and even its occurrence there was considered doubtful by Sledge. The first Bornean record was published by Copeland (1917, see synonymy), citing the localities Jesselton and Kudat, but not naming any specimens. There is indeed a specimen at MICH, *Topping* 1931, Jesselton (now Kota Kinabalu), collected in 1915. The species should be expected in Palawan and northwestern Luzon but has yet to be found in the Philippines.

Another species whose distribution almost completely rings the South China Sea but which is still awaiting discovery in Palawan or anywhere in the Philippines is *Pteris grevilleana* Wall. ex Agardh (additional Sabah specimen: *Beaman* 10587b, Ranau Dist., Bukit Lugas, Kg. Himbaan, 1250–1300 m, 5°57'N, 116°34'E).

Vittaria incurvata Cav., *Descr. pl.* 270. 1802; C. Chr., *Dansk Bot. Arkiv* 9(3): 24. 1937.

Although *V. incurvata* was described originally from Guam, many recent authors have inexplicably taken up later names, such as *V. elongata* Sw., described from southern India, in its stead for plants of Oceania and Malesia. Plants from Guam appear to differ from those of Sabah only by the paleae, in the former 7–12 mm long and subentire or minutely toothed only near base, in the latter 3–5 mm long and minutely toothed throughout. This difference might be sufficient to define a species in a difficult genus such as *Vittaria*; however, in islands near Guam, plants otherwise inseparable from topotypic *V. incurvata* have smaller and toothed paleae, which demonstrates that the Guam populations are at most a local variety. I am grateful to Dr. Lynn Raulerson of GUAM for sending me an excellent series of specimens from Guam, Saipan, Rota, Yap, and Palau for study.

SABAH SPECIMENS: *Beaman* 10569, Ranau Dist., Bukit Lugas, Kg. Himbaan, 1250–1300 m, epiphyte high on bamboo, 5°57'N, 116°34'E; *Clemens* 9486, 10007; *Topping* 1372, 1552.

ACKNOWLEDGMENTS

The Beaman collection was made possible by a Fulbright Fellowship at the Sabah Campus of the National University of Malaysia. Dean Ghazally Ismail of the Sabah Campus was particularly helpful in providing logistic support. The field work was assisted by Reed S. Beaman, Teofila E. Beaman, Pamla J. Decker, and others. Processing of specimens and subsequent research with the collection is supported by NSF grant BSR-8507843 to Michigan State University. Jacinto C. Regalado, Jr., searched through the entire collection to find the ferns and was constantly helpful. David M. Johnson, John H. Beaman, and Christiane Anderson reviewed the manuscript and made many useful suggestions, and Warren H. Wagner, Jr., provided advice on several topics.

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CAREX SECT. STELLULATAE (CYPERACEAE) IN THE NEOTROPICS

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INTRODUCTION

Reznicek & Ball (1980) revised *Carex* sect. *Stellulatae* (Kunth) Christ for North America but paid scant attention to the Neotropical representatives of the section. This paper provides a treatment of all the species that occur in Mexico, Central America, the West Indies, and South America. A key is provided to all Neotropical species. Neotropical endemics are described in full, but North American species that barely enter the region are not described and only briefly discussed. Members of *Carex* sect. *Stellulatae* can be distinguished from all other multiple-spiked members of subg. *Vignea* in the Neotropics by the combination of gynecandrous spikes and spreading to reflexed, planoconvex to biconvex, thick-margined perigynia.

Four species of *Carex* sect. *Stellulatae* are reported from the Neotropics: *C. angustior* Mackenzie, *C. interior* L. Bailey, *C. townsendii* Mackenzie, and *C. turumuquirensis* Steyermark. *Carex interior* is a very wide ranging North American species (Reznicek & Ball 1980) barely entering northern Mexico. The species was treated in detail and Mexican occurrences mapped in Reznicek & Ball (1980). *Carex turumuquirensis* is known only from the type locality in Venezuela. *Carex angustior* is reported from Hispaniola, and Mexico and Guatemala (Hermann 1974; Mackenzie 1931). The type of *C. angustior* is from the state of New York, and the name was placed in the synonymy of the circumboreal *C. echinata* Murray subsp. *echinata* by Reznicek & Ball (1980). *Carex townsendii* is endemic to the cordillera of Mexico and Guatemala and was not discussed by Reznicek & Ball (1980).

Carex turumuquirensis, though known from only one collection, appears to be a distinct species. The perigynia very closely resemble those of *C. interior*, but the more or less acuminate-awned lower staminate scales of the terminal spike set it clearly apart.

Carex angustior and *C. townsendii* both belong in what Reznicek & Ball (1980) termed the *C. echinata* complex. The six species of this complex recognized by Mackenzie (1931) as occurring in North America north of Mexico were reduced by Reznicek & Ball (1980) to one species with two subspecies. Mackenzie (1931) distinguished *C. townsendii* from all other members of the *C. echinata* complex by the combination of obtuse or obtusish, chestnut brown-tinged pistillate scales, phyllopodic culms, and thick, firm, and stiff leaf blades. Mackenzie, however, saw only the type collection. Hermann (1974) concisely summarized the differences universally used to separate *C. townsendii* and *C. angustior* in Mexico and Guatemala by the following couplet:

"Perigynia ovate, abruptly short-beaked, the beak less than half the length of the body.

C. townsendii.

Perigynia lanceolate, tapering into a beak more than half of to about the length of the body.

C. angustior."

Figure 1 shows a scatter diagram of perigynium beak length/body length versus perigynium length/width for all collections of the *Carex echinata* complex from Mexico and Guatemala (not more than two specimens plotted from any locality). Two groups corresponding to the two couplets quoted above are not evident. More striking is the considerable uniformity among specimens in these features, even though collected on different mountains and mountain systems. Figure 2, using the same axes, is based on a random sample of 50 perigynia from 50 culms of a single population sample from central Mexico (*Anderson 12946*). The variation from throughout Mexico and Guatemala in these perigynium features can be essentially matched by that within one large population. *Carex angustior* in Mexico and Guatemala, as in North America, is not a separable entity. Indeed, few collections from Mexico and Guatemala have lanceolate perigynia (L/W ratio = 3–6).

Based on the perigynium features noted above and all other features examined, Mexican and Guatemalan plants called *C. angustior* and *C. townsendii* are the same species. However, the relationship of these plants to north temperate representatives of *C. echinata* needs clarification. Mexican and Guatemalan plants are most similar to the variable circumboreal *C. echinata* subsp. *echinata*. A few points of distinction, however, are evident. Mexican and Guatemalan plants usually have dark inflorescences with pistillate scales dark brown with very narrow hyaline margins less than 0.1 (–0.2) mm wide. *Carex echinata* subsp. *echinata* usually has pale inflorescences with pale castaneous pistillate scales with broad hyaline margins 0.2–0.4 mm wide. Terminal spikes in Mexican and Guatemalan plants often are lacking a basal staminate portion or have one less than 2 mm long. *Carex echinata* subsp. *echinata* invariably has a staminate basal portion on the terminal spike (1–) 2–8 (–16.5) mm long (Fig. 3). Mexican and Guatemalan plants normally flower centrally, with fertile culms having old leaves of the previous year's vegetative shoot at their base. *Carex echinata* subsp. *echinata* usually flowers laterally, with bladeless sheaths at the base of the fertile culm. The latter difference, however, may be largely due to climate. Plants of *C. echinata* subsp. *echinata* from the very south of its range (e.g., coastal New Jersey) may also flower centrally, presumably because the apical meristem of the previous year's vegetative shoot is not killed by severe winter cold. Mexican and Guatemalan plants also do have stiff leaves, but this feature is difficult to assess and quantify in herbarium material.

None of the above characters alone provides a clear-cut separation of Mexican and Guatemalan plants but in combination allow most collections to be placed without reference to country of origin. The slight morphological differences of Mexican and Guatemalan plants from north temperate representatives of *C. echinata* argue against recognition at species rank. They are here recognized as a subtropical and tropical alpine subspecies, *C. echinata* subsp. *townsendii*, characterized by the separate geographical distribution and the minor morphological differences noted above.

The *Carex echinata* complex also occurs in the Neotropics on the island of Hispaniola in the West Indies. All collections from there, however, have pale

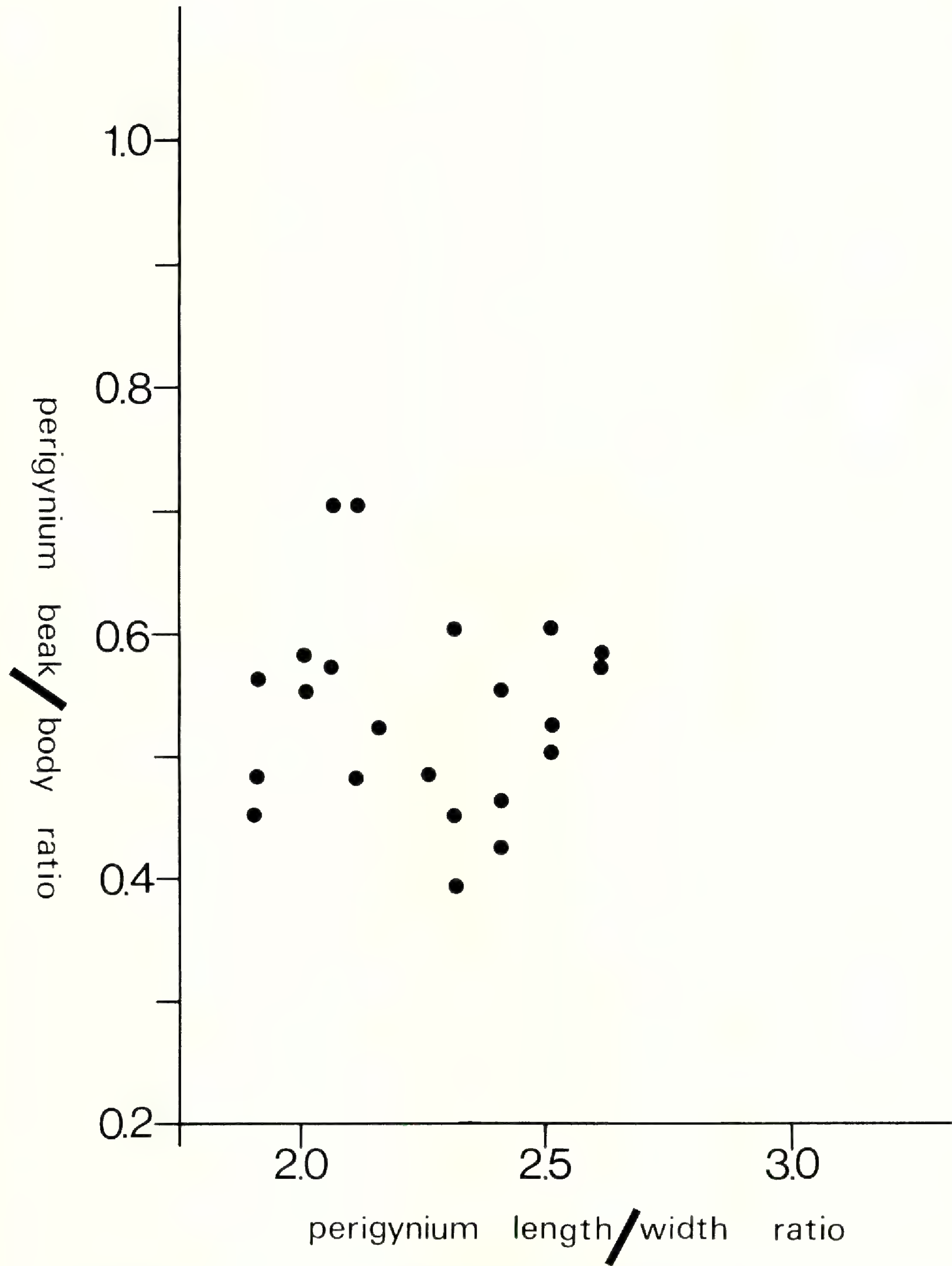


FIG. 1. Scatter plot of perigynium length/width ratio and perigynium beak length/perigynium body length ratio for *Carex echinata* subsp. *townsendii* from Mexico and Guatemala.

inflorescences and scales and staminate bases to the terminal spikes mostly 1.4–5.8 mm long. These collections are clearly referable to *C. echinata* subsp. *echinata*. All have very narrow leaves mostly 0.7–1.4 mm wide and small, narrow perigynia, and are essentially identical with the eastern North American plants, formerly segregated as *C. angustior*, that are of frequent occurrence from the

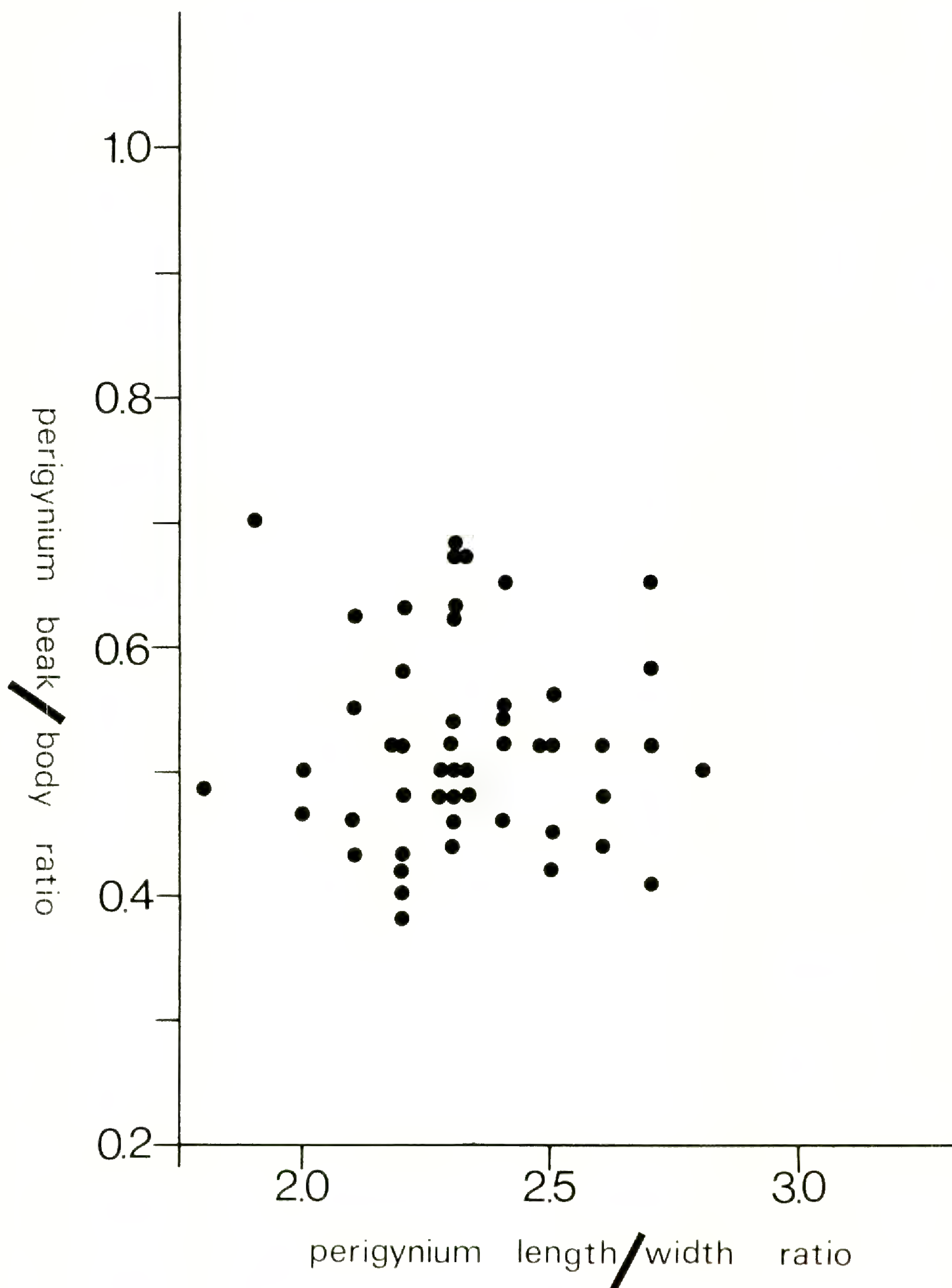


FIG. 2. Scatter plot of perigynium length/width ratio and perigynium beak length/perigynium body length ratio for *Carex echinata* subsp. *townsendii* from a random population sample of 50 perigynia from 50 inflorescences (from Anderson 12946).

southern Appalachian Mountains north to New England. The occurrence of a temperate North American *Carex* on a Caribbean island may seem odd, but odder still is that *C. echinata* subsp. *echinata* is not the only such species in the central cordillera of Hispaniola. *Carex limosa*, *C. leptalea*, *C. longii*, *C. lurida*, and *C. prairea* also occur there, for all but *C. longii* and *C. lurida* their only occurrence in the Neotropics.

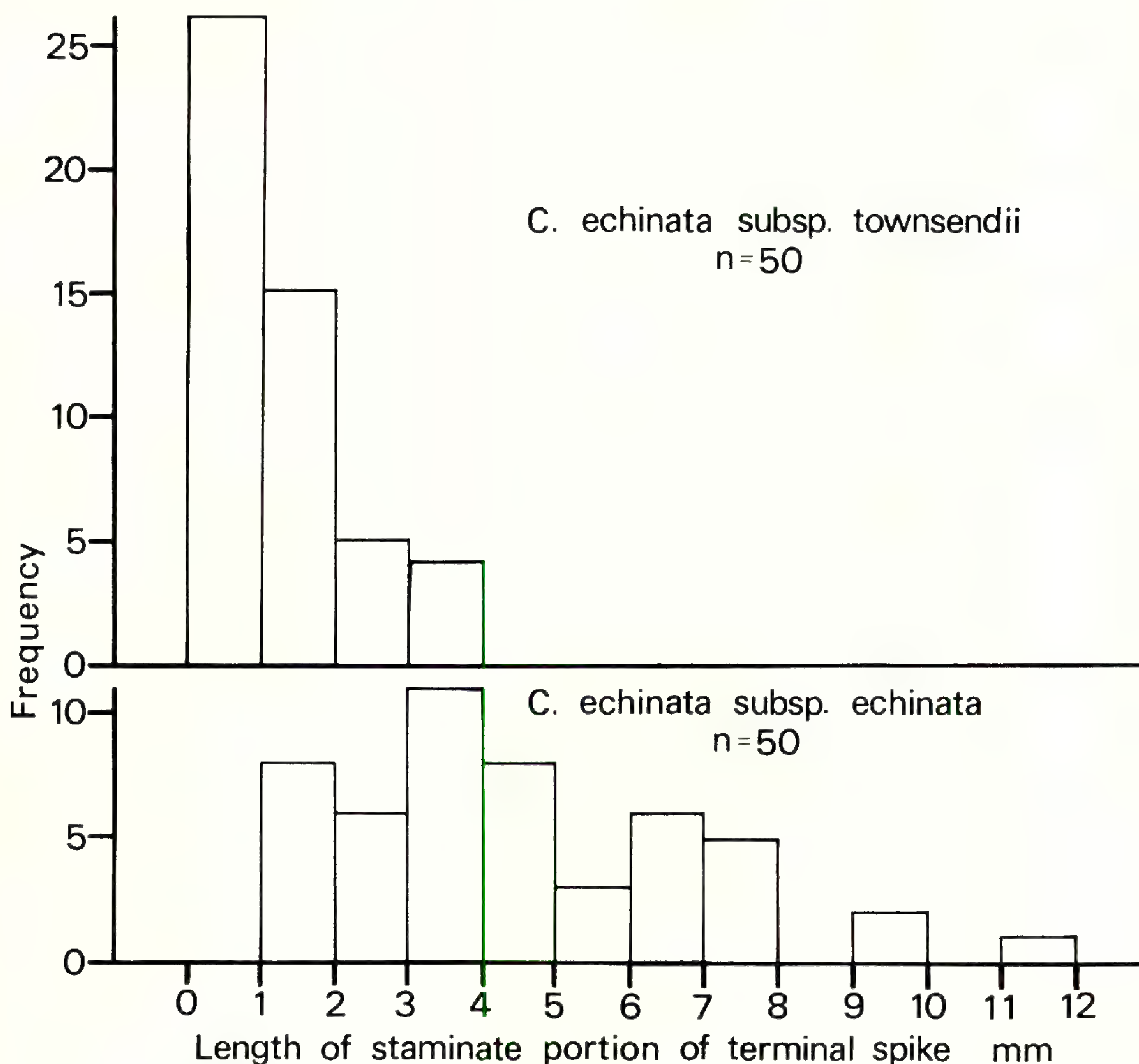


FIG. 3. Frequency diagram of the length of the staminate portion of the terminal spike of *Carex echinata* subsp. *townsendii* (top) and *C. echinata* subsp. *echinata* (bottom).

TAXONOMIC TREATMENT

1. Lower perigynia of spikes mostly 2–3.1 (–3.3) mm long; perigynium beaks 0.4–1 mm long; anthers mostly 0.6–1.2 (–1.4) mm long.
2. Lower staminate scales of terminal spike obtuse to acute; northern Mexico. 1. *C. interior*.
2. Lower staminate scales of terminal spikes acuminate to scabrous-awned; Venezuela. 2. *C. turumuquirensis*.
1. Lower perigynia of spikes mostly (2.65–) 2.8–4.6 mm long; perigynium beaks 0.9–1.8 mm long; anthers mostly (0.8–) 1.1–1.6 mm long.
3. Staminate portion of terminal spike absent or up to 2 (–5.5) mm long; pistillate scales usually castaneous to very dark brown with narrow hyaline margins up to 0.1 (–0.2) mm wide; Mexico and Guatemala. 3b. *C. echinata* subsp. *townsendii*.
3. Staminate portion of terminal spike (1–) 2–8 (–16.5) mm long; pistillate scales stramineous to pale castaneous with hyaline margins 0.2–0.4 (–0.6) mm wide; Hispaniola. 3a. *C. echinata* subsp. *echinata*.

1. *Carex interior* L. Bailey.

This species was described and discussed in detail in Reznicek & Ball (1980) and its distribution in the Neotropics mapped. The collection mapped by Reznicek & Ball from the Distrito Federal, Mexico, and alluded to by Hermann (1974) (*Rzedowski 20386*) has very dark scales and perigynium beaks ca. 0.9–1.1 mm long. This specimen is almost certainly a depauperate individual of *C. echinata*

subsp. *townsendii* and is cited here under that species. The southernmost dot in Mexico on the map in Reznicek & Ball, therefore, should be deleted.

2. ***Carex turumuquirensis*** Steyermark, Fieldiana: Bot. 28: 70. 1951.—TYPE: VENEZUELA. Sucre: Cerro Turumuquire, on ridge dividing headwaters of Río Manzanares and Río de Amana, 1900–2000 m, 10 May 1945, *Steyermark* 62704 (holotype: F!; isotypes: GH! NY! US!).

Plants cespitose, with short rhizomes; roots brown; fertile culms 15–45 cm tall, trigonous, erect to spreading, elongating in fruit, antrorsely scabrous-angled distally, with glabrous, pale brown basal sheaths. Leaves ca. 4–6, all in basal third; blades 8–25 cm long, 0.8–2.2 mm wide, flat to plicate, glabrous, margins antrorsely scabrous distally, the widest leaves 1.2–2.2 mm wide; leaf sheaths ca. 2–9 cm long, tightly enveloping culms, glabrous, green; inner band of sheaths hyaline, usually purple-dotted on lower sheaths, glabrous, apex concave; ligules 0.7–1.9 mm long, rounded, free portion thickened, stramineous. Vegetative shoots ca. 10–20 cm tall; leaves 4–6, similar to those on fertile culms; pseudoculms ca. 2–6 cm tall. Inflorescences 1.3–2.7 cm long, with the upper spikes overlapping and the lowest 2 spikes overlapping or separate, 3.1–6.8 mm distant; lateral spikes sessile; lowermost bracts 4–27 mm long, sheathless, lanceolate, prolonged into a green, scabrous, setaceous awn 2–25 mm long, the uppermost bracts much reduced. Spikes 3–7, gynecandrous or pistillate. Terminal spikes gynecandrous, 5.1–11.2 mm long; staminate portion 2.2–6.7 mm long, 0.8–1.3 mm wide, 4–11-flowered; pistillate portion 2.3–7.1 mm long, 4.3–5.3 mm wide, 2–12-flowered; sessile or on peduncles up to 3.9 mm long. Lateral spikes gynecandrous or pistillate, 3.2–6.9 mm long, 4.2–5.2 mm wide; staminate portion, if present, up to 2.3 mm long and 1–4-flowered; pistillate portion 2.6–5.8 mm long, 4–11-flowered. Pistillate scales 1.5–2.4 mm long, 1.1–1.8 mm wide, ovate, acute, glabrous, stramineous to pale castaneous with narrow hyaline margins up to 0.4 mm wide and green center, 1-veined. Staminate scales 1.7–3.5 mm long, 1–1.8 mm wide, narrowly ovate, acute to acuminate, the lowermost of the terminal spike sometimes prolonged into a scabrous awn up to 1.5 mm long, glabrous, stramineous to pale castaneous with narrow hyaline margins up to 0.2 mm wide and green center, 1-veined. Lower perigynia of spikes 2.4–3.1 mm long, 1–1.7 mm wide, spreading to more or less reflexed, planoconvex to slightly biconvex, ovate in outline, 1.7–2.4 times as long as wide, stramineous to castaneous, sessile, smooth-margined or serrulate on margins to 0.3 mm below base of beak, veinless or with up to 3 veins over achene adaxially, abaxially 6–12-veined over achene, spongy-thickened at base surrounding achene, contracted into a beak; beaks 0.7–1 mm long, 0.4–0.55 times as long as the body, stramineous to castaneous, serrulate on margins, the apex bidentulate with teeth up to 0.3 mm long. Achenes ca. 1.3–1.5 mm long, ca. 0.9–1.2 mm wide, biconvex, rhombic-ovate in outline, tightly enveloped by the perigynia, brown, sessile. Styles withering; stigmas 2. Anthers 3, 0.9–1.2 mm long.

Carex turumuquirensis was collected in a swampy meadow and is known only from the type collection. The type has spikes in mature fruit as well as ones just budding and ones far past maturity, thus fruiting probably occurs throughout the year.

Steyermark (1951) compared *C. turumuquirensis* quite accurately with *C. interior*. The thick-margined, small perigynia are certainly similar to those of *C. interior*; sufficiently so that individual perigynia of the two species could not be

reliably distinguished, although those of *C. turumuquirensis* are often narrower and slightly longer beaked. The consistent presence of a bract with a setaceous awn 2–25 mm long subtending the lowermost spikes also helps distinguish *C. turumuquirensis* from *C. interior*, which only rarely has a short setaceous awn on the lowermost bract. Representative inflorescences of *C. turumuquirensis* are shown in Figure 5.

3a. *Carex echinata* Murray subsp. *echinata*.

This subspecies was described and discussed in detail in Reznicek & Ball (1980) and its North American distribution mapped. In Hispaniola it occurs in wet places in open pine forest; seepy, grassy hillsides; "silt flats;" and other wet open sites from 1900–2900 m. Fruiting collections have been gathered from May through September. To the map in Reznicek & Ball (1980) must be added the localities in Hispaniola cited below.

SPECIMENS EXAMINED. HISPANIOLA. Santo Domingo; prope Constanza in Valle Nuevo, *von Türckheim* 3416 (NY); Valle Nuevo, *Augusto & Alain* 1492 (A, NY); Cordillera central, prov. de Azua, San Juan, Lomas de la Mediania, Sabaná Nueva, *Ekman* 13600 (A, GH, MICH, NY); Cord. Central, La Agüita, La Rucilla, *Liogier* 21729 (NY); Dominican Republic, La Vega: vicinity of Lagunita, *Gastony, Jones & Norris* 304 (GH, MICH, NY). San Juan: Sabaná Nueva, *R.A. & E.S. Howard* 9085 (GH, MICH, NY), 9095 (GH, NY).

3b. *Carex echinata* Murray subsp. *townsendii* (Mackenzie) Reznicek, comb. nov.

Carex townsendii Mackenzie, N. Amer. Fl. 18:111. 1931.—TYPE: MEXICO.

Chihuahua: Sierra Madre near Colonia García, 7500 feet, Jul 21 1899, *Townsend & Barber* 157 (holotype: NY!; isotypes: CAS! GH! MO! US!).

Plants caespitose, with short rhizomes; roots pale yellow to brown; fertile culms 10–65 cm tall, trigonous, erect to spreading, elongating in fruit, antrorsely scabrous-angled distally, with glabrous, pale brown basal sheaths. Leaves 4–8, all in basal third; blades 9–23 cm long, 1.4–2.8 mm wide, flat to plicate, glabrous to more or less papillose, usually more or less antrorsely scabrous on main veins adaxially, glabrous abaxially, the margins antrorsely scabrous distally, the widest leaves 1.6–2.8 mm wide; leaf sheaths 1.1–9.5 cm long, tightly enveloping culms, glabrous, green; inner band of sheaths hyaline, stramineous, sometimes faintly purple-dotted, glabrous, apex concave; ligules 0.8–1.7 mm long, rounded, free portion thickened, whitish to stramineous. Vegetative shoots ca. 6–33 cm tall; leaves 4–7, similar to those on fertile culms; pseudoculms ca. 2–11 cm tall. Inflorescences 1.1–3.9 cm long, with the upper spikes overlapping and the lowest 2 spikes overlapping or separate, 4.3–15 mm distant; lateral spikes sessile; lowermost bracts 3.6–27 (–45) mm long, sheathless, ovate, acuminate or more usually prolonged into a green, scabrous, setaceous awn 1.2–25 (–42) mm long, uppermost bracts much reduced. Spikes (2–) 3–8, gynecandrous or pistillate. Terminal spikes gynecandrous or pistillate, 4.4–11.8 mm long; staminate portion 0–2 (–5.5) mm long, 1.4–1.6 mm wide, 0–6 (–13)-flowered; pistillate portion 4.4–8.9 mm long, 5.6–8.5 mm wide, 7–26-flowered; sessile or on peduncles up to 2.2 mm long. Lateral spikes usually pistillate, 4.2–8.5 mm long, 5.3–8.7 mm wide; staminate portion, if present, up to 1.5 mm long and 1–3-flowered; pistillate portion 4.2–8.5 mm long, 5–17-flowered. Pistillate scales 1.9–2.9 mm long, 1.4–2.4 mm wide, ovate, obtuse to acute, glabrous, castaneous to very dark brown with narrow, hyaline margins up to 0.1 (–0.2) mm wide and green center, 1 (–3)-veined. Staminate scales 2.6–3.9 mm long, 1.4–2.1 mm wide, ovate,

acute, glabrous, pale castaneous to very dark brown with narrow, hyaline margins up to 0.1 (–0.2) mm wide and green center, 1 (–3)-veined. Lower perigynia of spikes (2.8–) 3.1–4.6 mm long, 1.3–2.1 mm wide, spreading to more or less reflexed, planoconvex, ovate in outline, 1.8–3.1 times as long as wide, stramineous to dark brown, sessile, smooth-margined or serrulate on margins to 0.7 mm below base of beak, usually veinless or rarely with up to 4 faint veins over achene adaxially, abaxially 3–14-veined over achene, spongy-thickened at base surrounding achene, contracted into a beak; beaks 0.9–1.8 mm long, 0.4–0.6 times as long as the body, stramineous to dark brown, serrulate on margins, the apex usually bidentulate with teeth up to 0.4 mm long. Achenes 1.4–1.9 mm long, 1.1–1.5 mm wide, biconvex, rhombic-ovate in outline, tightly enveloped by the perigynia, brown, sessile. Styles withering; stigmas 2. Anthers 3, 1–1.6 mm long.

Carex echinata subsp. *townsendii* occurs in open sedgy and boggy seeps, along streambanks in open pine forest, and in wet, open meadows from 2300–3800 m from Chihuahua, Mexico, to western Guatemala (Fig. 4). Fruiting occurs from late May through October. The range of this subspecies appears to be divided into three parts. The plant is locally frequent in western Guatemala and the transvolcanic belt in central Mexico; the type is the only known collection from Chihuahua. Although the sample of specimens is too small for positive conclusions, there appear to be no substantial differences in plants from these three areas, although the Chihuahua collection has slightly paler scales than most specimens from the other areas. A gap of about 1200 km separates the Chihuahua locality from the

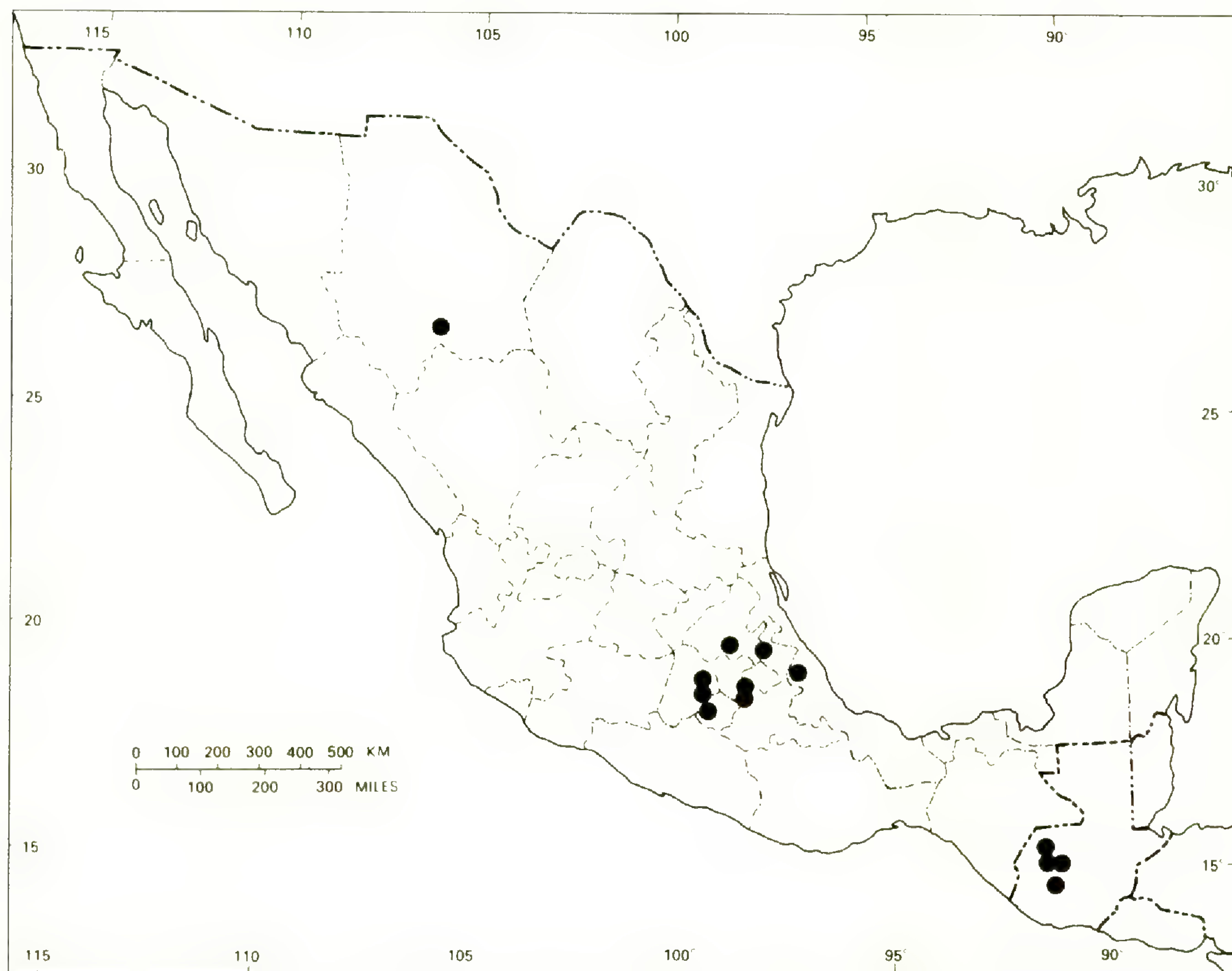
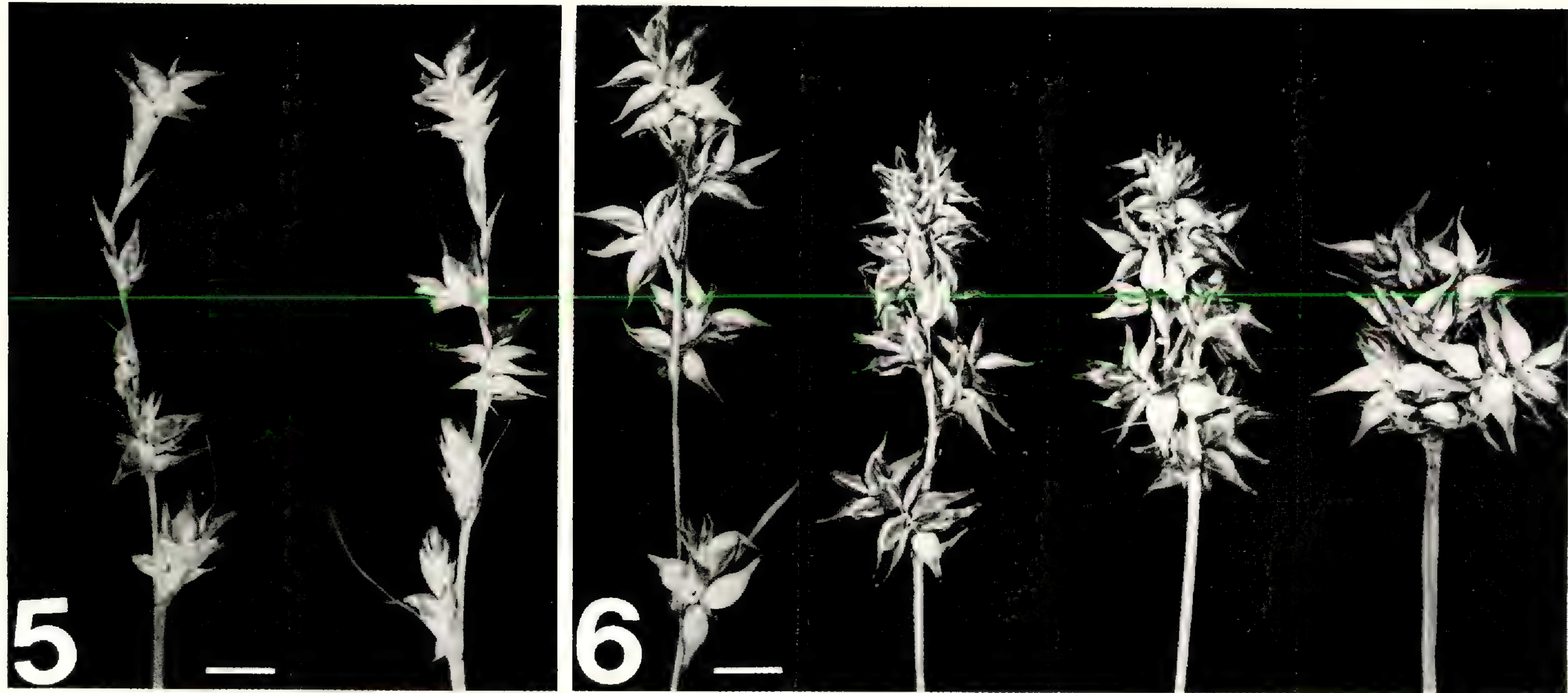


FIG. 4. Distribution of *Carex echinata* subsp. *townsendii*.



FIGS. 5–6. Representative inflorescences of *Carex turumuquirensis* and *C. echinata* subsp. *townsendii*; bar = 3 mm. 5. *C. turumuquirensis* (from Steyermark 62704). 6. *C. echinata* subsp. *townsendii* (from Anderson 12946).

nearest localities of *C. echinata* subsp. *echinata* in central Utah and Colorado and southern California.

With its dark scales and perigynia and terminal spikes often lacking a basal staminate portion, *C. echinata* subsp. *townsendii* might seem similar to the north-eastern North American *C. sterilis* Willd., but it can readily be distinguished by the narrow, usually less than 0.1 mm wide hyaline margins of the pistillate scales, the shorter anthers 1–1.6 mm long, the narrower perigynia 1.8–3.1 times as long as wide, and the smooth or only sparsely ciliate-serrulate margins of the perigynium body. *Carex sterilis* has broader hyaline margins 0.2–0.5 mm wide on the pistillate scales, anthers (1–) 1.2–2.2 (–2.35) mm long, perigynia 1.4–2.3 (–2.7) times as long as wide, and densely ciliate-serrulate margins on the perigynium body. *Carex sterilis* is also usually more or less dioecious. Representative inflorescences of *C. echinata* subsp. *townsendii* are shown in Figure 6.

SPECIMENS EXAMINED. GUATEMALA. Huehuetenango: alpine areas in vicinity of Tunimá, Sierra de los Cuchumatanes, *Steyermark* 48331 (F, GH); top of Cerro Chemalito, Sierra de los Cuchumatanes, *Steyermark* 49924 (F); Chiantla, between Llano de Musmul and Llano de San Nicolás, *Smith* 174 (F–2, MICH). Totonicapán: on the Tecum Uman Ridge at km 154 on Ruta Nacional No. 1, ca. 20 km east of Totonicapán, *Beaman* 4184 (ENCB, GH, MICH); Totonicapán, parcialidad Velasquez, *Smith* 827 (F).—MEXICO. Distrito Federal: Desierto de los Leones, *Lyonnet* 2145 (CAS, ENCB, MEXU–2, US), 2597 (ENCB, MEXU–2); 4°dinamo de contreras, *Rzedowski* 20386 (US); Llano de la Cienequilla, arriba del Desierto de los Leones, *González* 1107 (ENCB), 1108 (ENCB, MEXU); Delegación de Cuajimalpa, Puerto de las Cruces, *Rzedowski* 30808 (ENCB), 34273 (ENCB), 36722 (ENCB), *González* 997 (ENCB). Hidalgo: Sierra de Pachuca, *Pringle* 11364 (GH). México: 5 km al NW de Santa Ana Jilotzingo, *Rzedowski* 35121 (ENCB); south-west slopes of Volcán Ixtaccíhuatl along north side of Hwy 451 just below (W of) Parque Ixtapopo entrance, 2 km W of road jet. at Paso de Cortés, *T.S. & B.A. Cochrane* 8563 (ENCB, MEXU, MICH); Ladera NW del Popocatepetl, cerca del Paso de Cortés, *González* 1152 (ENCB); Mpio. de Amecameca, La Joya de Alcalicán, *Rzedowski* 36656a (ENCB), 36658a (ENCB), 36659a (ENCB); Mpio. de Iturbide, Presa Iturbide, 6 km al WNW de Santiago Tlazala, *Rzedowski* 35100 (ENCB); 2 km al SW de Santiago Tlazala, *González* 1119 (ENCB); Mpio. de Naucalpán, Villa Alpina, *Rzedowski* 35677 (ENCB, MEXU), 36153 (ENCB), 36156 (ENCB), 36159 (ENCB); Mpio. Ixtapaluca, Estación experimental de Investigación y Enseñanza de Zoquiapán, 8 km al S del Río Frío, *Koch* 75351 (ENCB, MEXU), *Vega* 234 (ENCB), 357 (ENCB, MEXU), *Galván* 699–B (ENCB), *Anderson* 12946 (MICH); entre Cerro Telapon y Cerro Tlaloc, *Arroyo* 274 (ENCB); Cañada de Temascatitla, 12 km al SSW de Río Frío, *Rzedowski* 37017 (ENCB). Morelos: Lago Zempoala, *Matuda* 25608 (NY). Puebla: Honey Station, *Pringle* 13293 (GH, MICH, US). Veracruz: Cofre de Perote, *Balls* B4776 (UC), B4631 (UC).

ACKNOWLEDGMENTS

I thank the curators of A, CAS, ENCB, F, GH, MEXU, MICH, MO, NY, UC, and US for allowing me to study their material. I also thank W. R. Anderson and S. D. Koch for providing the opportunity to observe and collect *Carex echinata* subsp. *townsendii*.

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OBSERVATIONS ON *LEPIOTA AMERICANA* AND SOME RELATED SPECIES

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The present contribution on *Lepiota* is part of a larger project on the macrofungi of the southeastern United States by Nancy S. Weber, Alexander H. Smith, and Dan Guravich. This report includes our observations on *Lepiota americana* and related species which have been reported from the study area or might be expected to occur in that area. One species, *L. besseyi*, is described as new and type studies and/or additional information are presented for *L. sanguiflua*, *L. tinctoria*, *L. americana*, and *L. jamaicensis*.

The fruiting bodies of species discussed here are gilled mushrooms with medium to large, thin-fleshed to moderately fleshy fruiting bodies. When bruised, the fruiting bodies typically exhibit a quick color change usually including some or all of yellow, orange, and deep dusky vinaceous red. They become dusky purple to vinaceous when dried. The pilear cuticle is initially continuous but breaks up as the pileus expands to form minute to large, innate scales arranged in somewhat concentric circles. The margin of the pileus may be short-striate at maturity. A distinct, membranous annulus is present on young specimens and often collapses in age. The spores are broadly ellipsoid to broadly ovoid and at most only faintly truncate from a minute apical pore, dextrinoid, metachromatic (the apical pore is pink in Cresyl blue in many spores), smooth, and thick-walled. Brachybasidioles are absent; cheilocystidia and, in one case, pleurocystidia, are present. The cheilocystidia are ventricose, most have a fingerlike apical projection that may fork and/or be constricted; their contents are light smoky gray as revived in KOH. NH_4OH turns the flesh green in those species that have been tested.

Although we have taken a conservative view and included all these species in the genus *Lepiota*, *L. americana* has been placed in *Leucocoprinus* (Redhead 1977) and the European species *Lepiota bresadolae*, considered by some to be a close relative of *Lepiota americana*, has also been placed in *Leucocoprinus* (Moser 1983; Wasser 1980). We (Smith & Weber 1982) have restricted *Leucocoprinus* to species whose fruiting bodies are thin and fragile, whose pileus is strongly striate to plicate-striate by maturity, and which possess brachybasidioles in the hymenium.

The collections studied are deposited in the University of Michigan Herbarium (MICH) unless otherwise noted. Color notations in quotation marks are taken from Ridgway (1912).

KEY

1. Pleurocystidia present, abundant. 1. *L. besseyi*.
1. Pleurocystidia absent. 2.
2. Umbo and scales on the pileus dark brown to blackish brown from buttons to maturity; cuticle of pileus over disc and in scales a distinct turf of $\pm$ erect pileocystidia (best studied in young specimens). 2. *L. sanguiflua*.
2. Not with both the above features. 3.
3. Scales on pileus minute, resembling tiny tufts of velvet; cuticle of pileus intermediate between a turf and a trichoderm, the end cells (pileocystidia) mostly with brown walls as revived in KOH and often with the tips adhering to one another. 3. *L. tinctoria*.
3. Scales on pileus small to large (over 5 mm in largest dimension), bran-like to fibrous; cuticle of pileus a mixture of variously inflated cystidioid cells and interwoven hyphae, the end cells sometimes forming a rudimentary trichoderm in very young specimens, trichoderm usually not evident in mature specimens, cells lacking brown walls or only scattered cells with brown walls. 4.
4. Cuticle and scales of pileus pinkish buff to pale pinkish cinnamon to light reddish brown, i.e., with a distinct dusky rose to pale cinnamon tone; flesh of fresh young specimens turning yellow then orange to orange red and finally dull reddish brown when bruised. 4. *L. americana*.
4. Cuticle and scales of pileus brown; flesh becoming reddish brown when bruised. 5. *L. jamaicensis*.

1. *Lepiota besseyi* H. V. Smith & N. S. Weber, sp. nov.—Pl. 1, Fig. 1a–e.

Pileus 2.5–9 cm latus, cuticula in squamas parvas, sordide rufulas vel cinnamonomeo-brunneas rumpens. Lamellae albae, ubi fractae rufae dein brunneae. Stipes 5–10.5 cm longus, 6–11 mm crassus, basin versus subamplificans, squamis fuscis, irregulatim dispersis vel in vittis partialiter cingentibus; squamae et superficies rufae dein brunneae ubi contusae; annulus armilloideus; superficies infera fusca. Sporae $9\text{--}11 \times 7\text{--}8 \mu\text{m}$, valde dextrinoideae, adsummum obscure truncatae; porus apicalis inconspicuus. Pleurocystidia abundantia, $66\text{--}80 \times 14\text{--}25 \mu\text{m}$, plerumque processu apicali, irregulari, digitiformi praedita. Cheilocystidia $35\text{--}70 \times 9\text{--}20 \mu\text{m}$, abundantia. Cuticula pilei disco e pileocystidiis elongatis, plerumque erectis composita. Pileocystidia (45–) $90\text{--}230 \mu\text{m}$ longa, $9\text{--}20 \mu\text{m}$ diametro in parte latissima, ambitu plus minusve irregulari; paries subbrunneus vel brunneus in KOH, basin versus fuscus. Conferti sub *Musa* sp. in cortice detricto Pini. Holotype: *D. Guravich* 802, Lake Jackson, Brazoria Co., Texas, 17 July 1976 (MICH).

Pileus 2.5–9 cm broad, in buttons truncate-ovoid to rounded conic, expanding to convex or plane at maturity; cuticle remaining intact over the disc longer than elsewhere, soon breaking up into minute to small scales away from disc, these more widely separated near the margin than near the disc, $\pm$ superficial (not incorporating much underlying tissue), scales and disc dull reddish brown to cinnamon-brown or sometimes darker (to fuscous), tissue between scales white to pale buff; margin incurved slightly when young, straight at maturity and then sometimes faintly striate at the very edge. Context 2.5–4 mm thick, soft, white to light buff, staining red to orange-red when bruised, finally reddish brown, odor fragrant, taste acidic. Lamellae free, close, white to pale buff, quickly changing to red or orange-red when bruised, finally dull reddish brown after several minutes. Stipe (3.5–) $5\text{--}10.5 \times (4.5\text{--}) 6\text{--}11$ mm, slightly enlarged to subbulbous toward the base, tapered toward the apex, white and glabrous to thinly appressed fibrillose above the annulus, below annulus with irregular patches and bands of tissue resembling the pileus cuticle in color and texture, ground color white to pale buff, soon staining orange to red and then brown where bruised or cut; rhizomorphs numerous at the base. Veil typically forming an annulus, sometimes leaving frag-

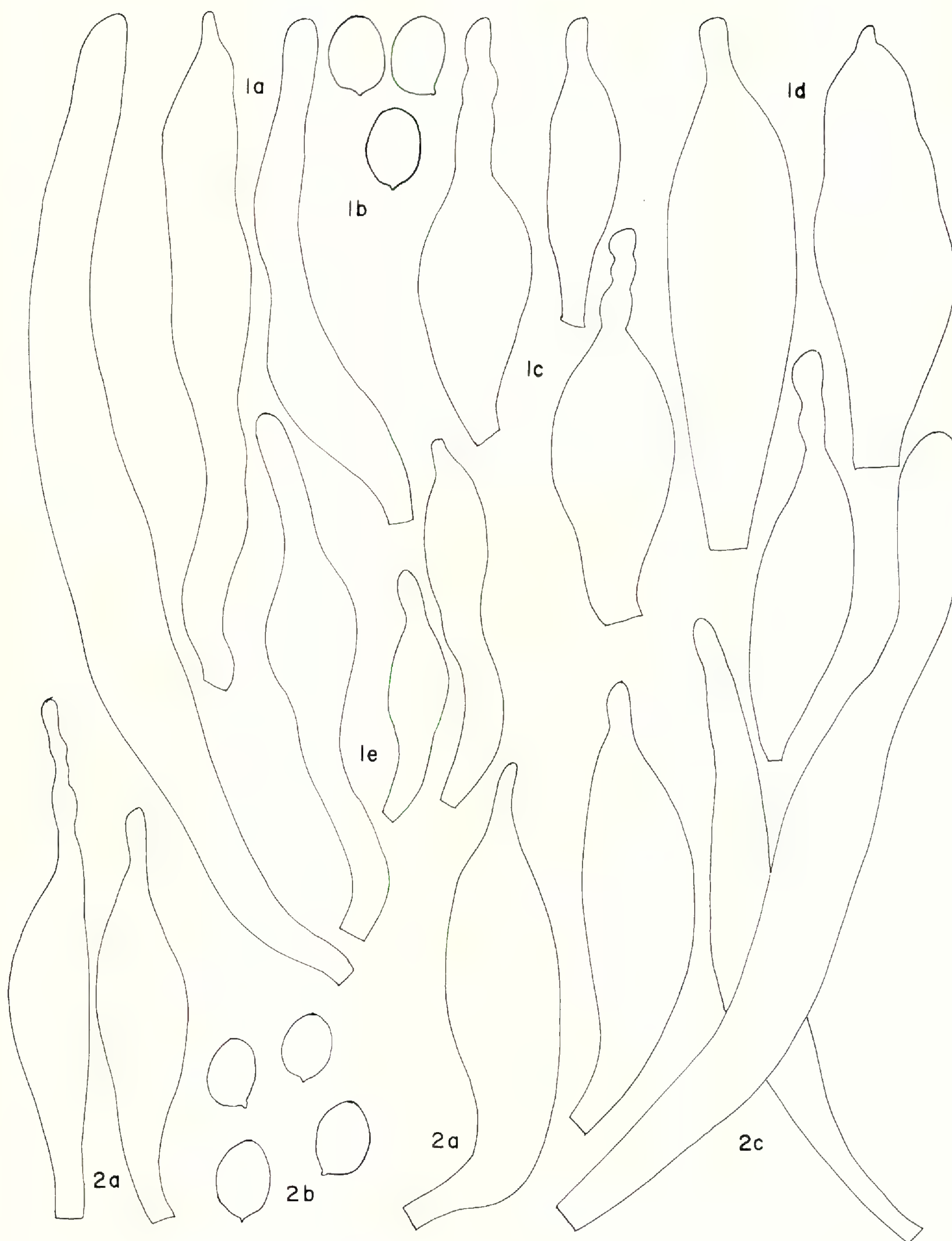


PLATE 1. Fig. 1, *L. besseyi* (Guravich 802): a, pileocystidia; b, spores; c, cheilocystidia; d, pleurocystidia; e, caulocystidia. Fig. 2, *L. sanguiflua* (Murrill F 18298): a, cheilocystidia; b, spores; c, pileocystidia. Spores $\times 500$, others $\times 400$.

ments on the margin of the pileus, annulus flaring at first, collapsing against the stipe or evanescent in age, lower surface colored like the disc of the pileus. Chemical reactions (from *Ovrebo 1898*): 10% KOH: darkens brownish; 10% NH_4OH : turns quickly green then after 4–5 minutes turns gray with a pinkish halo at edge of gray.

Spores in deposit dark creamy buff. Spores (from sections) $9\text{--}11 \times 7\text{--}8 \mu\text{m}$;

broadly ovate to broadly ellipsoid, dextrinoid, metachromatic, smooth, thick-walled, at most only obscurely truncate from an inconspicuous apical pore. Basidia $27\text{--}39 \times 9\text{--}12 \mu\text{m}$, 4-spored. Pleurocystidia abundant, $(55\text{--}) 66\text{--}80 \text{ (}\text{--}90) \times 14\text{--}25 \mu\text{m}$, arising in the subhymenium, broadly fusoid or clavate to, typically, ventricose, often abruptly enlarged where they extend beyond the basidia, usually developing an irregular fingerlike apical projection by maturity, contents pale smoky brown to grayish tan as revived in KOH. Cheilocystidia $35\text{--}70 \times 9\text{--}20 \mu\text{m}$, abundant but not making the gill edge sterile, similar to the pleurocystidia in shape and content. Lamellar trama loosely interwoven. Pilear cuticle over disk a turf of elongate basically erect pileocystidia arising from interwoven hyphae, the layer pulling apart as the pileus expands, the resulting scales formed of tufts of pileocystidia. Pileocystidia $(45\text{--}) 90\text{--}230 \text{ (}\text{--}240) \mu\text{m}$ long, $9\text{--}20 \mu\text{m}$ in diameter at widest part, elongate, variable and irregular in shape, often enlarged below, tapered toward the apex or with a rounded apex; wall light to medium brown as revived in KOH, darkest toward the base, bands of pigment present on scattered hyphae below the pileocystidia. Clamp connections not observed. Stipe ornamentation composed of clusters of caulocystidia $18\text{--}90 \mu\text{m}$ long, $6.9\text{--}27.6 \mu\text{m}$ in maximum diameter; caulocystidia elongate, versiform, most clavate to ventricose, with or without a mucro or fingerlike apical projection, walls of many dark to light brown as revived in KOH, contents often light cinnamon-brown.

MATERIAL STUDIED: HAWAII: *E. A. Bessey* 8, in a lawn near Agricultural Hall on University of Hawaii Campus, Honolulu, Oahu, 30 Oct 1939.—LOUISIANA: *C. Ovrebo* 1898, on lawn & leaf mulch, Tulane University Campus, New Orleans, Orleans Parish, 22 Oct 1985 (NO).—TEXAS: *D. Guravich* 802, clustered under banana [plant], growing in pine bark chip mulch, Lake Jackson, Brazoria Co., 17 Jul 1976 (TYPE, MICH).

We take pleasure in naming this species for *E. A. Bessey*. In his notes he observed that: "This species is very closely related to *L. americanus* [sic] but appears to be readily distinct by virtue of its abundant pleurocystidia. The margin of the pileus does not appear to be striate, nor the stipe as characteristically bulbous, but these characters may not be constant." The pleurocystidia are the most distinctive feature of the taxon. In the Guravich and Bessey collections the notes and/or photographs indicate more or less reddish brown to cinnamon tones on the pileus whereas Ovrebo noted fuscous tones; in all collections the walls of the pileocystidia are light to dark brown as revived in KOH, and we suspect the differences may reflect different responses to weathering and handling. The structure of the pilear cuticle is very similar to that of *L. sanguiflua* and *L. bresadolae*. Those species with fine, superficial scales tend to have a turf for a cuticle; those, such as *L. americana*, with coarser scales have more interwoven hyphae and contextual hyphae in the scales. All parts of the fruiting bodies that were white when fresh are dull reddish purple to vinaceous brown or darker brown after drying. The type collection is illustrated in color in Weber et al. (1985, pl. 144).

2. *Lepiota sanguiflua* Murrill, Quart. J. Florida Acad. Sci. 8: 179. 1945.—Pl. 1, Fig. 2a–c; Pl. 3, Fig. 1a.

Pileus 2.3–9.3 (–11) cm broad, thin and fragile, broadly conic in buttons, expanding through convex to plane, with or without a prominent umbo at maturity; cuticle soon breaking up into minute to small fibrillose scales toward the margin, often continuous over the disc, scales fewer and more widely spaced

toward the margin and sometimes absent from the margin; margin obscurely striate by maturity; disc and scales blackish brown ("bone brown", "warm sepia" or "bister"), exposed context white or nearly so, scales and surface fibrils staining reddish orange or rusty orange when rubbed. Context very thin, white to pallid, staining yellow where injured and orange when chewed, taste mild at first, then slightly biting or pungent. Lamellae faintly pale yellow ("cream buff"), bright yellow where injured by insects, close, moderately broad. Stipe 7.5–12 cm long, 4–9 mm at apex, 7–14 mm at base, equal to slightly clavate, minutely scurfy-furfuraceous over all, off-white at first but the base becoming yellow to salmon-orange to brownish where handled or in age, the ornamentation soon darkening and colored like the scales of the pileus to "saya brown" or "snuff brown". Annulus bandlike, often ascending, thin, white on the upper surface, colored like the disc of the pileus on the lower surface, collapsing in age and then absent or present as a thin appressed dark brown zone.

Spore deposit when heavy distinctly pale yellow. Spores (from deposit) $7.5\text{--}10.5 \times 5.5\text{--}6.5$ (~ 7.5) μm , (in sections, larger spores, $12\text{--}15 \times 7.2\text{--}8$ μm , are not uncommon), broadly elliptic in face view, elliptic to obscurely inequilateral in profile, at most only faintly truncate from a minute apical pore, dextrinoid, metachromatic, smooth; apiculus minute. Basidia $21\text{--}24 \times 9\text{--}10.5$ μm , 4-spored. Pleurocystidia not observed. Cheilocystidia $30\text{--}52 \times 10\text{--}15$ μm , clavate to broadly fusoid ventricose, most with a crooked or constricted fingerlike projection up to 12 μm long, contents as revived in KOH diffusely pale brown. Exposed pilear context between the scales of hyphae which often branch, round off, and separate at the septa. Intact pilear cuticle a turf of elongate more or less erect pileocystidia (60--) $90\text{--}207 \times 18\text{--}26$ μm ; pileocystidia versiform-elongate, often slightly inflated in the lower half and tapered toward the apex, or clavate, walls of many cells dark brown over all as revived in KOH, contents also often grayish brown. The turf is pulled apart as the pileus expands, and the resulting scales are formed of tufts of pileocystidia which are arranged in clusters with the bases close together and the apices spreading. Caulocystidia $90\text{--}184 \times 13\text{--}26$ μm , in tufts, clavate varying to ventricose with an apical projection, walls and contents (especially in young specimens) brown as revived in KOH.

MATERIAL STUDIED: FLORIDA: *W. A. Murrill, F 18289* (TYPE, FLAS), in rich soil under a live-oak in Gainesville, Alachua Co., 20 Aug 1944.—HAWAII: *E. A. Bessey 7*, in troops or clusters in grass, Waikiki Beach, Oahu, 30 Oct 1939.—MICHIGAN: *A. H. Smith 67687*, on sawdust and wood debris in a millyard, Marquette, Marquette Co., 20 Sep 1963, *leg. I. Bartelli*.—MISSISSIPPI: *D. Guravich 1362*, on a leaf pile, Gulf Coast Research Laboratory, Ocean Springs, Jackson Co., 13 Jul 1981; *D. Guravich 1364*, cespitose to scattered on a shaded compost pile, same locality as 1362, 15 Jul 1981, both *leg. N. S. Weber and D. Guravich*.—NEW YORK: *F. J. Seaver*, in conservatory, New York Botanical Garden, Bronx, Sep 1942.

The specimens of *Guravich 1364* were predominantly white except for the scales when removed from the mushroom drier; 4 days later they were dusky rose. This observation agrees with Murrill's statement that his specimens showed a slow change from white to rose in the herbarium. Of the specimens cited above, all those collected before 1981 have lost their dusky rose color and are muddy ochraceous.

The combination of slender stature of the fruiting bodies, thin flesh, blackish brown disc and scales on the pileus, and color change from yellow to orange of injured parts of the fruiting bodies helps distinguish this species.

3. *Lepiota tinctoria* Murrill, Lloydia 6: 223. 1943.—Pl. 3, Fig. 3a–d.

Pileus 5–10 cm broad, somewhat conical at first, becoming broadly conic to expanded convex with a low broad umbo, cuticle smooth and continuous over the disc, ruptured into numerous small to minute scales which are widely scattered toward the margin; margin obscurely striate; disc pale to dark pinkish brown (pale chestnut according to Murrill), scales similar or paler, the surface between the scales white; context thin, quickly yellow then darker when cut. Odor pleasant, taste somewhat acrid. Lamellae white, free, quickly yellow when touched or cut, then pinkish brown, later dark gray (Murrill). Stipe 5–10 cm long, 6–10 mm thick, slightly clavate, glabrous or nearly so above, below the annulus scaly and brown, staining quickly yellow when handled, then pinkish brown to slowly blackish brown at the base. Annulus white above, colored like the pileus below, flaring or collarlike, persistent.

Spores (from sections) $(7.5-)$ 9–10.5 $\times$ $(5.5-)$ 6–8 μm , broadly ellipsoid to ovate in face view, obscurely inequilateral in profile, dextrinoid, metachromatic, smooth, thickwalled with a minute apical pore which scarcely makes the spore truncate. Basidia about 35 μm long. Pleurocystidia not observed. Cheilocystidia 22–75 $\times$ 9–17 μm , abundant, clavate to somewhat ventricose, most with a fingerlike apical projection which may have 2–3 constrictions or be forked, contents diffusely grayish tan as revived in KOH. Pilear cuticle over disc in buttons approximately 160–230 μm thick, intermediate between a turf and a trichoderm of erect hyphae, the end cells elongate, cystidioid, many pileocystidia clavate or otherwise enlarged, some with a short fingerlike projection, many cells with brown walls; toward the margin the layer pulling apart to form the scales, the apical cells of the pilear cuticle often clumped at their tips and thus collapsing toward the center of the scale as the layer stretches out. Pilear cuticle in expanded specimens often a recognizable trichoderm over the disc and in the scales but usually in various stages of being pulled apart and collapsing, walls of many cells brown near and at the base, lighter toward the apex, most end cells cystidioid, to 92 $\times$ 19 μm , often in tufts, apical proliferations of cystidioid cells longer in older specimens and often matted over the surface. Clamp connections very rare. Caulocystidia clavate to ventricose or fusoid ventricose, often with a apical proliferation, to 120 $\times$ 25 μm .

MATERIAL STUDIED: FLORIDA: *Murrill, F 19944* (ISOTYPE, MICH; HOLOTYPE, FLAS), cespitose on a shaded lawn, Gainesville, Alachua Co., Sep 11, 1942.—MISSISSIPPI: *Guravich 402*, cespitose on lawn in area where an oak tree had been removed 2 years earlier, Greenville, Washington Co., 31 Aug 1974; *402a*, same locality as 402, 1 Sep 1974.—TEXAS: *Hillhouse 303*, in rich humus on a lawn under loblolly pine, St. Augustine, Brazoria Co., Sep 1, 1974.

The principal differences between this species and *L. americana* were noted by Murrill as follows: “Closely related to *L. americana* but with much smaller scales. It stains the fingers yellow at once when handled. After some days in the herbarium the gills turn dark-gray while the rest of the hymenophore is pale-chestnut.” Specimens in both the Hillhouse and Guravich collections turned vinaceous instead of chestnut on drying except for the gills, which have a slightly metallic gray cast to them. Compared to the fruiting bodies of *L. americana*, those of *L. tinctoria* are much more slender, and have much smaller scales. Specimens of *L. americana* are typically fleshier and have larger, more fibrous scales on the pileus. The structure of the pilear cuticle provides the easiest way of separating the two species. Our discussion of the cuticle of the pileus is based on

studies of the isotype at MICH. The paler colors and more highly developed trichoderm of *L. tinctoria* are useful in separating specimens of it from those of *L. sanguiflua*.

4. *Lepiota americana* (Peck) Peck, Ann. Rep. New York State Mus. 49: 56. 1897.—Pl. 2, Fig. 2a–d.

Agaricus americanus Peck, Ann. Rep. New York State Cab. 23: 71. 1872.

Leucocoprinus americanus (Peck) Redhead in Groves, Publs. Dept. Ag. Canad. 1112, ed. 2: 323. 1979.

Pileus (3–) 6–15 (–30) cm broad at maturity, in buttons truncate-ovoid to ovoid, expanding through campanulate to broadly convex or plane, with or without a low broad umbo; margin slightly incurved at first, straight to slightly upturned and sometimes striate by maturity. Pilear cuticle entire and smooth to slightly roughened or suedelike over all at first, remaining intact over the disc, separating elsewhere into flat to slightly recurved fibrillose scales which are least dense near the margin; pinkish buff to pale pinkish cinnamon darkening to dull vinaceous cinnamon or light reddish brown; ground color white to pale buff; injured areas in young, freshly gathered specimens typically first changing to bright yellow then orange to orange-red and finally dull vinaceous to brownish where handled, older specimens may not stain yellow to orange before changing to reddish brown. Context thin, soft and cottony, coloring as above; when touched with NH_4OH becoming dark grayish green. Odor and taste not distinctive. Lamellae free but approximate to the stipe when young, creamy white to pale yellow (“marguerite yellow”), broad, thin, edge finely fimbriate, all parts changing color as above when injured. Stipe (7–) 8–12 (–14) cm long, (0.6–) 1.2–2.2 (–4) cm in diameter at largest point, usually fusiform-ventricose with the enlarged portion below the midpoint then abruptly “pinched off” at the base but sometimes merely clavate or nearly equal, glabrous and unpolished above, glabrous to sparsely longitudinally fibrillose below, in dry weather often cracked and scaly near the base; creamy white above the annulus, pallid to tinged vinaceous or concolorous with the disc below, staining like the pileus when bruised; rhizoids often present at the base. Annulus median to superior, membranous, flaring, sometimes collapsing or evanescent, whitish, the lower margin colored like the pileus and staining like it when bruised.

Spore print pale cream color (ivory or “cartridge buff”). Spores (from sections) (7.9–) 9–10.5 (–12) $\times$ 6.3–7.5 (–9) μm , broadly elliptic to subglobose in both face and profile view or very slightly tapered toward the rounded apex, at most only faintly truncate from a small apical pore; dextrinoid, metachromatic, smooth, thick-walled. Basidia 27–36 $\times$ 8–12 μm , 4-spored. Pleurocystidia not seen. Cheilocystidia 75–120 $\times$ 12–18 μm , abundant, clavate to ventricose with or without an apical projection, projections short to moderately long, flexuous or somewhat moniliform; contents typically pale smoky brown as revived in KOH. Pilear cuticle in buttons approximately 300–400 μm thick, of interwoven to ascending hyphae sometimes forming a rudimentary trichoderm with the upper cells but often the arrangement not so precise, many cells at least slightly inflated, slender hyphal tips often matted on the surface, no distinct pileocystidia observed, walls of cells in upper part of cuticle often pale brown. In age, cuticle similar, some of the large cells may be embedded pileocystidia; the layer pulling apart irregularly to form the scales. Scales that have been teased apart appear composed of cylindric, clavate, broadly ellipsoid, or fusoid-ventricose cells 77–138 μm

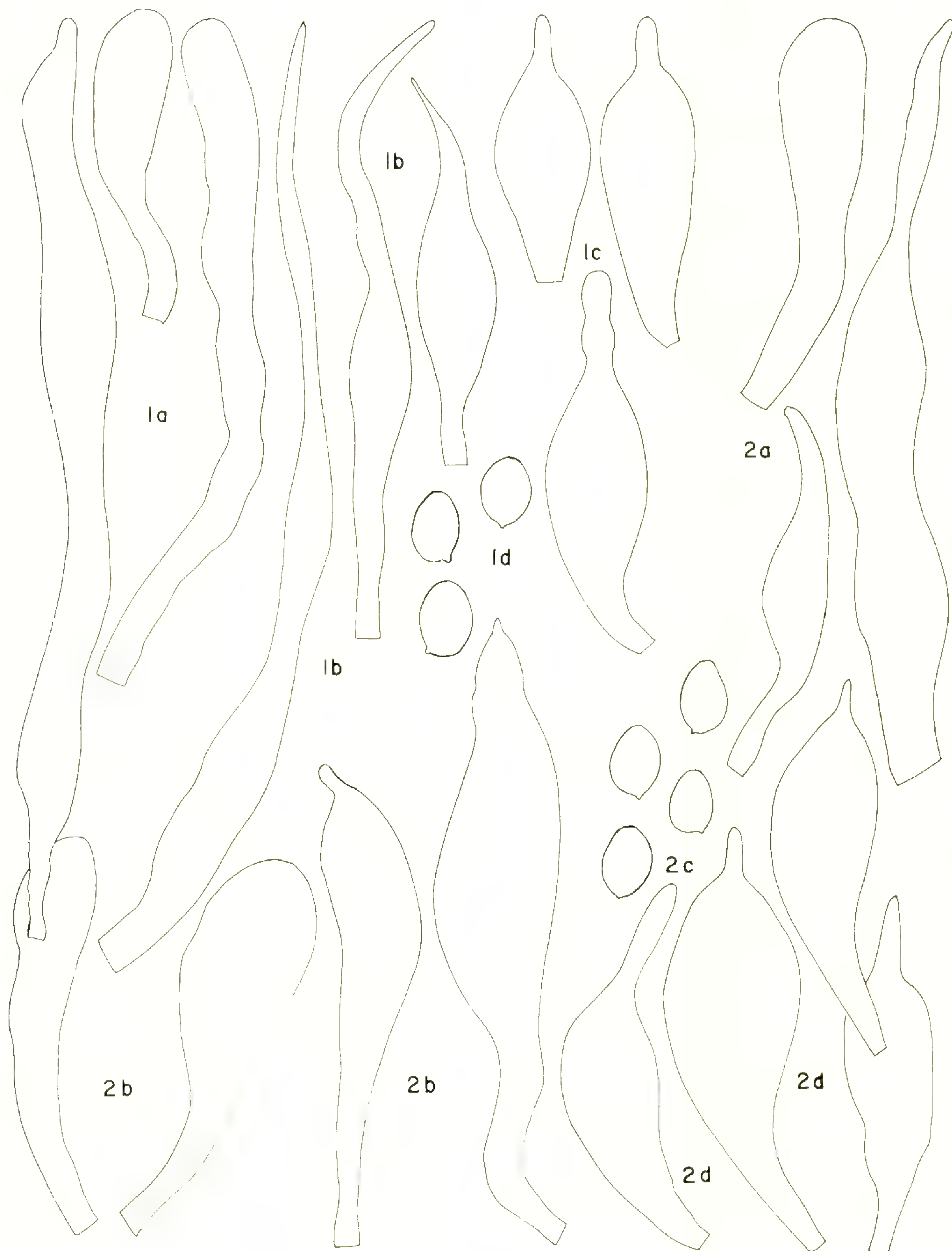


PLATE 2. Fig. 1, *L. bresadolae* (Moser 82/378): a, pileocystidia; b, caulocystidia; c, cheilocystidia; d, spores. Fig. 2, *L. americana*: a, caulocystidia (K. H. Harrison 6618), b, pileocystidia; c, spores; d, cheilocystidia; (2b–d from G. W. Clinton collection). Spores $\times 500$, others $\times 400$.

long and up to 25 μm in diameter mixed with narrower hyphae. Exposed context between scales of radially arranged hyaline hyphae which may separate at the sepa. Clamp connections rare (see discussion below).

MATERIAL STUDIED: MICHIGAN: K. A. Harrison 6618, Ann Arbor, Washtenaw Co., 3 Jul 1962; K. A. Harrison 9698, old lumberyard, Alder Creek area, Marquette Co., 10 Sep 1970, leg. K. A.

Harrison & J. F. Ammirati; C. Ovrebo, 4 Oct 1979, growing from woodchip pile, Haven Hill, Highland Recreation Area, Oakland Co.; *A. H. Smith 67667*, in a millyard, Marquette, Marquette Co., 20 Sep 1963, leg. *I. Bartelli; H. V. Smith 468*, on a sawdust pile, Haven Hill, Highland Recreation Area, Oakland Co., 20 Sep 1975, leg. *N. S. Weber; H. V. Smith 521*, on decaying wood, Univ. of Michigan campus, Ann Arbor, Washtenaw Co., 6 Aug 1963, leg. *G. Pacione & A. H. Smith*.—NEW YORK: *G. W. Clinton*, grassy ground by roadsides, Buffalo, Aug (TYPE, NYS).—VIRGINIA: *O. K. Miller 18549*, Blanchard's lawn, Blacksburg, Montgomery Co., 26 Sep 1979, leg. *H. Miller* (VPI). *O. K. Miller 19178*, Blacksburg, Montgomery Co., 27 Sep 1980, leg. *E. Castro-Mendoso* (VPI).

Lepiota americana is widely distributed in eastern North America. It usually fruits during warm, wet weather in the summer and early fall on or near rotting wood, around stumps, where woody material has been buried, on piles of sawdust, or on ground heavily mulched with wood chips. The collections listed above are representative collections and not meant to be a complete list of those studied.

All parts of the fruiting bodies become dull vinaceous to vinaceous-brown when dried or soon thereafter—this color change may take a day or two to develop fully—and the color change seems to persist for many years. Clamp connections were not found in most of the collections studied nor in the portion of the holotype examined. However, in *H. V. Smith 468* they were found on several consecutive septae and a few were scattered elsewhere. The presence of isolated or rare clamp connections in a so-called “clampless” species is not uncommon in other genera of fleshy fungi according to Alexander H. Smith (pers. com.). *Lepiota americana* is considered to be an edible mushroom; it has the interesting ability to turn milk in which it is cooked blood-red. It likewise, if eaten in quantity, is said to turn the urine red.

L. americana is the central species, historically, in this group in North America. The others have mostly been defined on the basis of how they may differ from it. Several types of pilear cuticle can be found in the group and can be arranged in a series from the turf of *L. besseyi* and *L. sanguiflua* through the poorly developed trichoderm of *L. tinctoria* to the complex and irregular arrangement of elements in the cuticle of *L. americana*. The European species *L. bresadolae* Schulzer [*Leucocoprinus bresadolae* (Schulzer) Wasser or Moser—both published the combination the same year and we have not been able to discover which was first], as interpreted by Moser (1983) and Jossierand (1974), is also a member of this group. In the absence of a type collection for *L. bresadolae*, we studied the microscopic features (Pl. 2, fig. 1a–d) of *Moser 82/378* (Umgebung von Redipuglia, Gorizia, Italien, zw. Laub, 1982–10–02, IB). In this collection, the pilear cuticle consists of a turf of versiform elongate pileocystidia, many of whose walls were light to dark brown at least at the base. Pleurocystidia were not observed. The fresh material, as shown in a color photograph, had a pale pinkish cinnamon cast to the scales and disc of the pileus, and the flesh stained yellow then red when injured. The pilear cuticle broke up into very small, superficial scales. The structure of the pilear cuticle is more similar to that of *L. sanguiflua* and *L. besseyi* than *L. americana*.

5. *Lepiota jamaicensis* Murrill, Mycologia 3: 87. 1911.—Pl. 3, Fig. 2a–d.

We know this species only from Murrill's description and our study of the holotype (at NY):

“Pileus 10 cm. in diameter, convex to plane, with a prominent hemispherical umbo, cespitose on dead wood, the entire sporophore becoming reddish-brown when bruised or on drying; surface dry, white or very pale yellowish, adorned

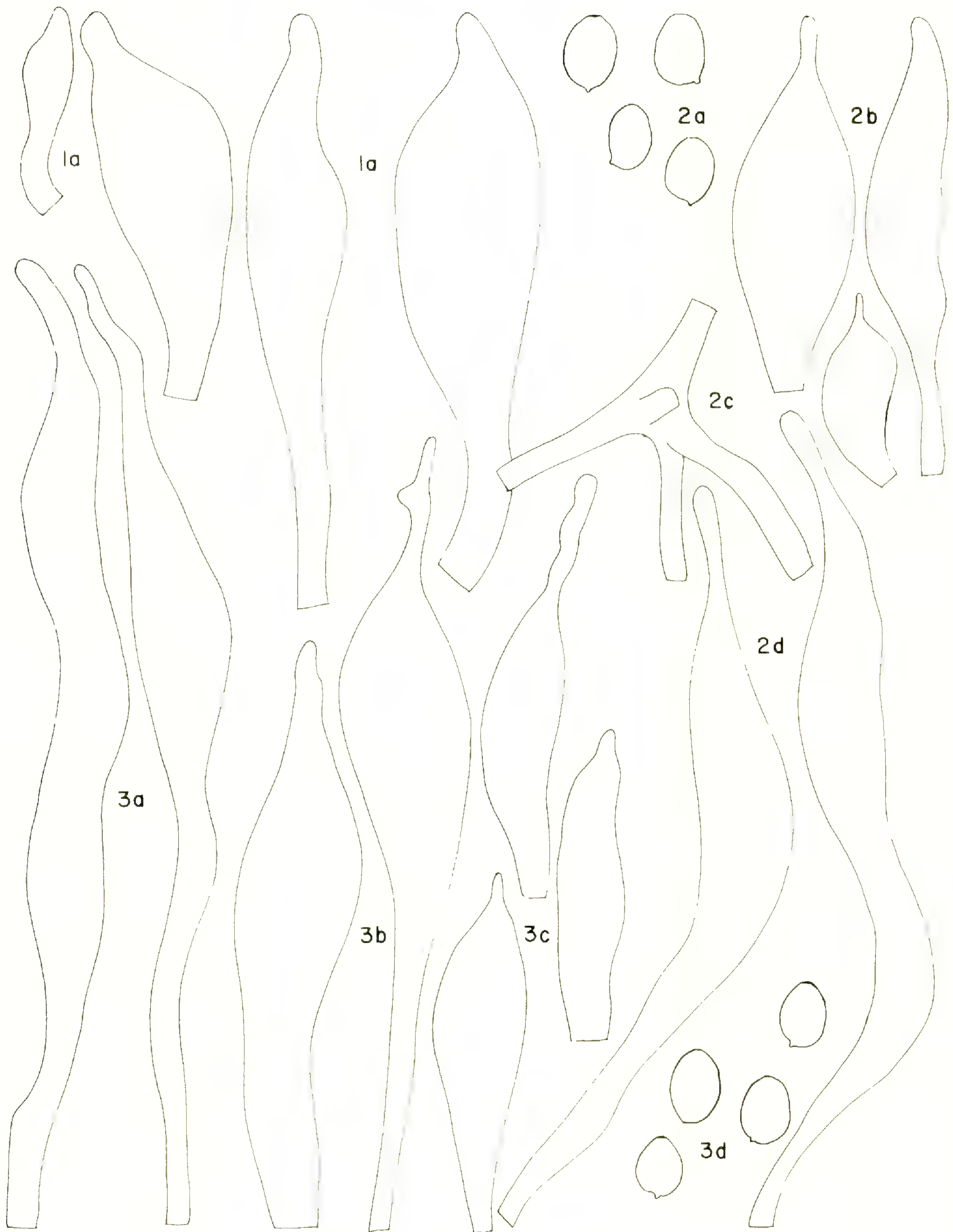


PLATE 3. Fig. 1, *L. sanguiflua* (Guravich 1364): a, caulocystidia. Fig. 2, *L. jamaicensis* (Murrill 181): a, spores; b, cheilocystidia; c, branched cell from pileus; d, pileocystidia. Fig. 3, *L. tinctoria* (Murrill F 19944, MICH): a, pileocystidia; b, caulocystidia; c, cheilocystidia; d, spores. Spores $\times 500$, others $\times 400$.

with brownish, floccose scales 1 mm broad, the remains of the cuticle; umbo brown, minutely scaly; context thin, white; lamellae free, white, becoming discolored when the spores mature; spores ovoid, rounded at both ends, not apiculate, often uninucleate, very pale brown $9 \times 6-7 \mu\text{m}$; stipe enlarged at the base, tapering upward, 10 cm or more long, 1.7 cm thick below, 0.7 cm thick above, subglabrous, slightly reddish-brown; annulus large, superior, moveable, reddish brown.

"Type collected on a hardwood stump in a cocoanut plantation near Manchioneal, Jamaica, at an elevation of about 100 m, December 17, 1908, W. A. Murrill 181.

"This plant closely resembles *Lepiota americana* Peck, a well-known temperate species, both in shape and color, but grows in dense clusters on dead wood, has decidedly browner spores, and much smaller scales on the pileus, as well as a minutely scaly umbo. Its affinities are evidently with *Lepiota*, although the spores are not altogether hyaline."

Spores $9\text{--}10.5 \times 6\text{--}7.5 \mu\text{m}$, broadly ellipsoid, dextrinoid, metachromatic, thick-walled with a small apical pore. Pleurocystidia not observed. Cheilocystidia reviving poorly, $48\text{--}62 \times 12.6\text{--}20 \mu\text{m}$, clavate to ventricose, many with an apical fingerlike projection, content pale brownish gray in KOH. Basidia 4-spored (or a few appearing to be 2-spored), $20\text{--}27 \times 8\text{--}9 \mu\text{m}$, stout. Pilear cuticle near disc of expanded pileus and in scales of hyphae with large cystidioid end cells, the pileocystidia $95\text{--}140 \times 9\text{--}17 \mu\text{m}$, not forming a distinct turf but clustered as if originating in a trichoderm, elongate and variable in shape including fusoid ventricose, ventricose and clavate, most with a fingerlike apical projection, walls of some cells light brown especially near the base of the cell. Hyphae of exposed context between scales with numerous branched cells that round off at the septa, and separate readily under slight pressure. Clamp connections not observed.

The distinctions used in the key to separate *L. americana* and *L. jamaicensis* are admittedly tenuous; it is a strong possibility that if *L. jamaicensis* could be restudied from fresh material that no basis for recognizing two taxa would be found. We have maintained the distinction based on color change, because Murrill saw the fresh material and presumably would have noticed a change to yellow if one had been evident. The color of the spores is not distinctive in this group; we have examined many specimens in which spores deposited on the cap or on the gills are pale honey-colored to pale golden brown as revived in KOH.

ACKNOWLEDGMENTS

The directors and staff of the Matthaei Botanical Gardens and the Herbarium generously allowed us to use their facilities. Alexander H. Smith provided many pertinent suggestions during the preparation of the manuscript. The junior author's field work was aided by Dr. Harold Howse, who made the facilities of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi available. David P. Lewis, Clark Ovrebo, and William Cibula contributed data, collections, and discussions that were most helpful. We thank those who have made collections in other herbaria available to us, particularly the curators at FLAS, IB, NO, NY, NYS, and VPI. Meinhard Moser read an earlier version of this paper and made useful comments on it; he also shared data in the form of specimens and photographs of *L. bresadolae* with us. We are particularly indebted to Ellen Thiers who graciously prepared the Latin description of *Lepiota besseyi*.

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RECORDS AND NOTES ON ALASKAN MARINE ALGAE. II.

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Ongoing investigations of the benthic marine algal flora of Alaska have resulted in some observations concerning collections made at Amchitka Island in the Aleutians and in southeast Alaska. The present paper details findings on some species newly recorded for the Pacific Ocean: *Sphacelaria caespitula* Lyngbye and *Myriocladia lovenii* J. Agardh. It also includes the first reports of the occurrence in Alaska of *Ceramium cimbricum* H. Petersen, *Neorhodomela aculeata* (Perestenko) Masuda, *Feldmannia simplex* (P. & H. Crouan) Hamel, *Pilayella littoralis* (Linnaeus) Kjellman f. *rupicola* (Areschoug) Kjellman, and *Acrothrix gracilis* Kylin. Additional information is provided concerning *Callithamnion acutum* Kylin, *Cryptopleura ruprechtiana* (J. Agardh) Kylin, and *Sphacelaria rigidula* Kützinger. Voucher specimens of these collections made by the author have been deposited in the University of Michigan Herbarium (MICH), Ann Arbor.

RHODOPHYTA

CERAMIACEAE

Callithamnion acutum Kylin.

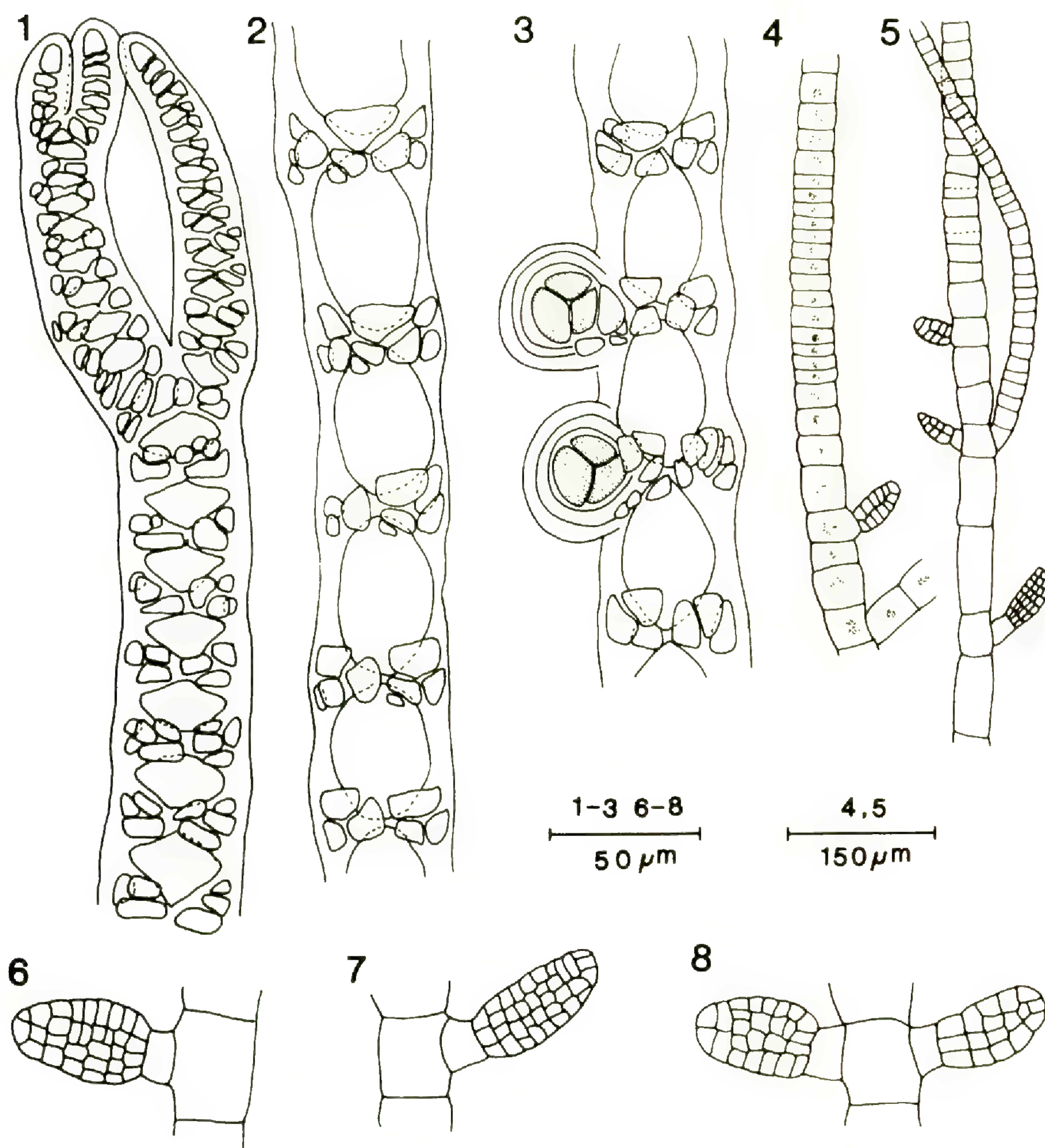
ALASKA: Wynne 6268–A, 9.viii.1980, island east of Heceta Island (55°47'34"N, 133°27'54"W), southern Sea Otter Sound, Prince of Wales Island; tetrasporic. *Lebednik* AM–249, 13.iv.1969, Constantine Harbor dock, (51°24'35"N, 179°19'00"E), Amchitka Island, Aleutians; tetrasporic.

Abbott and Hollenberg (1976) treated *C. californicum* Gardn. as a later taxonomic synonym of *C. acutum*, and I agree with this judgment. This species has been previously known from Alaska as *C. californicum* (Lindstrom 1977).

Ceramium cimbricum H. Petersen in Rosenvinge (Figs. 1–3).

ALASKA: Wynne 5387 and 6264, 9.viii.1980, east side of Heceta Island (55°48'05"N, 133°29'49"W), southern Sea Otter Sound, Prince of Wales Island.

This species was described by H. Petersen (in Rosenvinge 1923–24) from two localities in the Limfjord of Denmark and has more recently been reported for The Netherlands (Stegenga & Mol 1983). It is also distributed in the western North Pacific: Sakhalin (Tokida 1948), northern Japan (Nakamura 1965), Korea (Kang 1966), and the Japan Sea (Perestenko 1980). The distinguishing features include the straight, often unequal apices (Fig. 1), the very narrow cortical bands, consisting of (1–) 2 (–3) transverse rows of cells (Fig. 2), the cells in the lower edge of the cortical bands having parallel upper and lower sides, and the tendency toward a creeping habit. The Alaskan material is in good agreement with the previous accounts of the species.



FIGS. 1-8. Figs. 1-3, *Ceramium cimbricum*; Figs. 4-8, *Feldmannia simplex*. Fig. 1. Apices of erect axes. Fig. 2. Portion of axis with nodal cortication. Fig. 3. Axis bearing tetrasporangia. Figs. 4, 5. Axes with zones of cell division. Figs. 6-8. Examples of plurilocular sporangia.

Although fertile material has apparently not been reported in European material, tetrasporic and cystocarpic specimens are known in the Pacific populations. In agreement with the observations of Tokida (1948), the tetrasporangia in the Alaskan specimens are extruded and essentially naked (Fig. 3), except for a few small cortical cells near their attachment. The sporangia are arranged usually in a row on the adaxial side of the upper branches. The occasional whorls of sporangia reported by Tokida (1948) and Nakamura (1965) were not observed in the Alaskan collection. Female and cystocarpic specimens were described by Nakamura (1965) and Perestenko (1980).

The thalli are both creeping and erect. Plants reach a height of 2 cm. Rhizoids arise from the cortical cells. Vesicle cells or hair cells are not present. These collections represent the first record of this species for Alaska (and the eastern North Pacific).

Although *C. cimbricum* has been placed in the synonymy of *C. diaphanum*/*C. strictum* (e.g., Sjöstedt 1928), Lucas (1953) asserted that *C. cimbricum* can be

distinguished from *C. diaphanum* (Lightf.) Roth by the presence of 4–5 periaxial cells in the former and 6–8 periaxial cells in the latter. I observed four periaxial cells per segment in the Alaskan specimens.

DELESSERIACEAE

Cryptopleura ruprechtiana (J. Agardh) Kylin.

ALASKA: *Wynne 5087*, 28. vii. 1980, Pirate Cove (56°59'15"N, 135°22'00"W), 5 mi SW of Sitka, on W coast of Baranof Island. *Wynne 5221*, 27. vii. 1980, Three Entrance Bay (56°58'40"N, 135°22'40"W), 5.5 mi. SW of Sitka, on W coast of Baranof Island. *Wynne 5436*, 10. viii. 1980, near Gas Rock (55°50'26"N, 133°33'24"W), southern Sea Otter Sound, Prince of Wales Island.

Whether this alga should be assigned to *Cryptopleura* or *Botryoglossum* is a persistent taxonomic problem. The oldest valid name for this species is *Hymenena fimbriata* used by Postels and Ruprecht (1840) for an alga they described from Norfolk (=Sitka) Sound, Baranof Island, Alaska, and also occurring on the Kamchatka Peninsula. In his treatment of a broadly defined *Nitophyllum*, J. Agardh (1872, 1876) used the substitute name *Nitophyllum ruprechtianum* for the North Pacific species, because the name *Nitophyllum fimbriatum* was already occupied by a species described from Brazil by Greville (1833). DeToni (1900) used the name *Botryoglossum ruprechtianum* (J. Ag.) DeToni, an incorrect name, since the combination *Botryoglossum fimbriatum* would be called for if this species were to be assigned to that genus. Some authors, however, have used that name (Hollenberg & Abbott 1966; Abbott & Hollenberg 1976; Lindstrom 1977). Kylin (1924) transferred both the North Pacific species and the Brazilian species to *Cryptopleura*, using *C. ruprechtiana* for the former species and *C. fimbriata* for the latter. Scagel (1957, 1967), Widdowson (1974), and Hawkes et al. (1978) have accepted *C. ruprechtiana* to designate the North Pacific species.

In *Botryoglossum*, based on its South African type *B. platycarpum* (Turn.) Kütz., male, female, and tetrasporic reproductive structures are restricted to small bladelets (fertile proliferations) borne often in clusters on the surfaces or margins of the primary blades (Turner 1811; Wagner 1954). In *Cryptopleura*, based on its type *C. ramosa* (Hudson) Kylin ex Newton [= *C. lacerata* (Gmelin) Kütz.] tetrasporangial sori are borne in marginal proliferations, but procarps/cystocarps are produced randomly over the primary blade surfaces (Kylin 1924, as *C. lacerata*; Stegenga & Mol 1983). Kylin (1924, 1956) attempted to segregate taxa into *Botryoglossum* or *Cryptopleura* on the basis of the origin of tetrasporangia: only from cortical cells in *Botryoglossum* or from both cortical and primary cells in *Cryptopleura*. Such a generic distinction has been found to be untenable by Wagner (1954) and Ver Steeg & Josselyn (1983). The latter authors concluded their study by proposing the transfer of *Botryoglossum farlowianum* (J. Ag.) DeToni to *Cryptopleura*, but their transfer was invalid in their failure to cite the basionym.

In their original account of *Hymenena fimbriata*, Postels and Ruprecht (1840, pl. 40, fig. 64) described and illustrated the cystocarps to be located along the margin of the primary blade. They also referred to the fimbriate nature of the margin. Subsequent authors (Abbott & Hollenberg 1976) have shown the tetrasporangial sori to be produced in these marginal fimbriae, or proliferations. Based on the nature of the location of the cystocarps and tetrasporangial sori, this

species cannot be assigned to *Botryoglossum*, which has its fertile proliferations scattered over the surface of the blade, nor to *Hymenena*, which has tetrasporangial sori arranged over the primary blade. This species is thus correctly assigned to *Cryptopleura* on the basis of the tetrasporangial sori on marginal proliferations and the cystocarps being on the primary blade, not on special fertile outgrowths.

Another taxonomic problem concerns the relationship of *Cryptopleura ruprechtiana* to *C. farlowiana*; these two species overlap one another in their distributional ranges. Abbott and Hollenberg (1976) distinguished California populations by the more delicate thalli and the discrete rather than ruffled marginal proliferations in *C. ruprechtiana*. But Hawkes et al. (1978), studying populations from British Columbia, recognized a "morphological continuum" between these two species and called them a single species, *C. ruprechtiana*. Ver Steeg and Josselyn (1983) did not address the question of how *C. farlowiana* can be distinguished from *C. ruprechtiana*. For the Alaskan material under discussion the correct name is *Cryptopleura ruprechtiana*, the provenance of the type locality being Sitka Sound, southeast Alaska.

RHODOMELACEAE

Neorhodomela aculeata (Perestenko) Masuda.

ALASKA: Wynne 5234, 31.vii.1980, Silver Bay (57°02'N, 135°12'W), 5 mi E of Sitka, Baranof Island; tetrasporic. Wynne 5291, 8.viii.1980, Cape Suspiro (55°27'30"N, 133°08'30"W), 1 mi S of Craig, on W coast of Prince of Wales Island. Wynne 5541, 11.viii.1980, Sandy Beach, 10 km north of Thorne Bay (54°41'N, 132°31'W), Clarence Strait, Prince of Wales Island. Wynne 5568, 12.viii.1980, west spit of Fish Egg Island (55°29'20"N, 133°10'15"W), NW of Craig, Prince of Wales Island.

This species has not previously been reported for Alaska. This taxon was originally described by Perestenko (1967) as a subspecies of *Rhodomela larix* (Turner) C. Ag. Prior to that it has passed under the name *Rhodomela larix* in northern Japan and adjacent waters, but according to Masuda (1982) genuine *R. larix* does not occur in the western North Pacific. The most recent taxonomic opinion was Perestenko's (1984) treatment of this taxon as *Neorhodomela larix* subsp. *aculeata*.

Masuda (1982) segregated the genus *Neorhodomela* from *Rhodomela* C. Ag. on the basis of the vegetative and fertile trichoblasts being arranged in a zigzag manner in two rows along the abaxial convex side of the main axes and lateral branches. Thus, they are dorsally positioned in contrast to the spiral arrangement of the trichoblasts in *Rhodomela*. The distribution of the type of *Neorhodomela*, *N. munita* (Perestenko) Masuda, is restricted in the western North Pacific. *Neorhodomela larix* (Turner) Masuda is a very common alga ranging along much of the Alaskan coastline, southward to southern California (Abbott & Hollenberg 1976). The only prior record of *N. aculeata* for the eastern North Pacific was Masuda's (1982) report of its occurrence at Bamfield, Vancouver Island, Canada. The main axes of *N. aculeata* are covered with setaceous determinate branches, to 10 mm long and less than 0.5 mm broad, unlike the thicker determinate branchlets in *N. larix*. Indeterminate branches are developed in the axils of the determinate laterals in the mid-region of the main axes. Dorsally arranged trichoblasts were observed at the apices of the main axes and the lateral branches.

Neorhodomela oregona (Doty) Masuda, which has a somewhat comparable North Pacific distribution (northern Japan, the Aleutians, Oregon, and northern California), is distinguishable from *N. aculeata* on the basis that the first-order branches in *N. oregona* grow indeterminately, whereas the vast majority of first-order branches in *N. aculeata* are determinate, remaining simple (Masuda 1982).

PHAEOPHYTA

ECTOCARPACEAE

Feldmannia simplex (P. & H. Crouan) Hamel (Figs. 4–8).

ALASKA: Wynne 5505, 9.vii.1980, northeast end of Heceta Island (55°47'26"N, 133°27'54"W), southern Sea Otter Sound, Prince of Wales Island.

This species was first recorded in the Pacific by Norris & Wynne (1969) on the basis of a collection made in Washington. Those authors agreed with the suggestion made by Cardinal (1964) that the Pacific *Ectocarpus cylindricus* Saunders was conspecific with the Atlantic *F. simplex*. Evidence was offered to demonstrate that the morphological characteristics of these two taxa overlapped significantly. More recently Abbott & Hollenberg (1976) have continued to recognize *F. cylindrica* (Saund.) Abb. & Hollenb. from California but did not present any evidence for the distinctiveness of that species.

The Alaskan collection occurred as an epiphyte on *Codium ritteri* Setch. *Codium* is commonly the host for *Feldmannia simplex*. As in European specimens (Sauvageau 1933), plurilocular sporangia are conical, obtuse, and typically produced on one-celled pedicels (Figs. 6–8); they are arranged either singly or in opposite pairs on the sparsely branched axes. Zones of growth are conspicuous (Figs. 4, 5), as is characteristic of the genus. Numerous discoid chloroplasts each bearing a pyrenoid were also observed.

Giffordia ovata (Kjellm.) Kyl. also occurs in the northeastern North Pacific (Norris & Wynne 1969; Hawkes et al. 1978; Hansen et al. 1981) and can be easily confused with *Feldmannia simplex*. *Giffordia* is distinguished from *Feldmannia* by the absence of discrete zones of growth in the former genus. But such zones of growth are reported for *G. ovata*, which includes *G. intermedia* (Rosenv.) Lund, according to Pedersen (1979). Pedersen (1979) stated that the zones of growth in *G. ovata* are restricted to the base of pseudohairs. Furthermore, branching in *G. ovata* occurs along the length of the erect filaments (Rosenvinge & Lund 1941); whereas branching in *F. simplex* is concentrated at the base of erect filaments, with no branching or production of reproductive organs above the zones of growth. Reproductive organs tend to be sessile and arranged in opposite pairs in *G. ovata* (Rosenvinge & Lund 1941). Despite these differences it seems that these two species, *F. simplex* and *G. ovata*, are closely related.

Pilayella littoralis (Linnaeus) Kjellman f. **rupincola** (Areschoug) Kjellman.

ALASKA: Wynne 5148-A, 29.vii.1980, northwest part of Siginaka Islands (57°09'N, 135°27'W), 8 mi. NW of Sitka, Baranof Island. Wynne 3018, 13.viii.1970, St. Makarius Bay (51°22.0'N, 179°14.7'E), Amchitka Island, Aleutians.

This forma, which has been recognized at the species level by some workers (e.g., Levring 1937), has not previously been reported from Alaska. Its first

report for Pacific North America was made by West (1967), who recorded it from San Juan Island, Washington. Its distinctive features include its tendency toward "cable-rolling" and the apparently exclusive production of unilocular sporangia.

SPHACELARIACEAE

Sphacelaria caespitula Lyngbye (Figs. 9, 10).

ALASKA: Wynne 6295, 9.viii.1980, east side of Heceta Island, southern Sea Otter Sound, Prince of Wales Island.

This appears to be the first record of *S. caespitula* in the Pacific Ocean. Previously, it was known only from Europe (Prud'homme van Reine 1982). It is placed in subgenus *Sphacelaria*, in which propagules are lacking. Thus, it is related to *S. radicans* (Dillw.) C. Ag., which was recently reported to also occur in Alaska (Wynne 1985). But these species can be distinguished by the conspicuous presence of pericysts and the greater diameter of the filaments in *S. radicans* (Prud'homme van Reine 1982). In the Alaskan specimens of *S. caespitula* the mature filaments measure 28–32 μm in diameter (Fig. 9). Plurilocular sporangia are present (Fig. 10).

Sphacelaria rigidula Kützinger.

ALASKA: Wynne 6303, 8.viii.1980, Cape Suspiro, Craig, Prince of Wales Island.

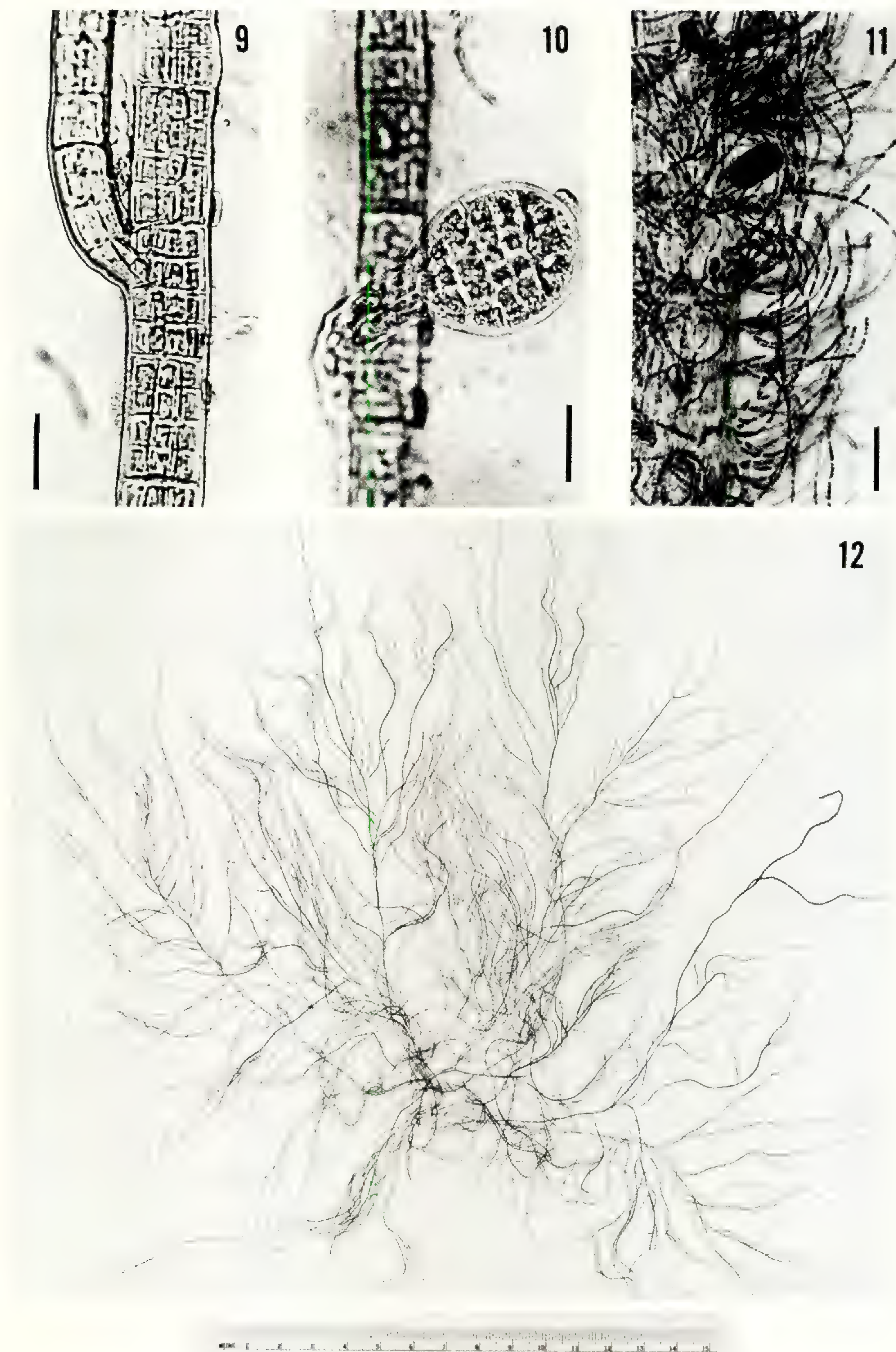
Prud'homme van Reine (1982) has shown that *S. rigidula* Kütz. (1843) is an earlier taxonomic synonym of *S. furcigera* Kütz. (1855), the latter being a familiar name for a widely occurring alga. Although Setchell & Gardner (1925) used the number of arms on the propagules, namely, strictly two in *S. furcigera* and two or three in *S. subfusca* S. & G., Prud'homme van Reine (1982) indicated that the propagules of *S. rigidula* have (1–) 2–3 (–4) arms. Thus, there seems little justification to recognize *S. subfusca*, which has been reported from Alaska (Setchell & Gardner 1925; Johansen 1971; Calvin & Lindstrom 1980).

CHORDARIACEAE

Myriocladia lovenii J. Agardh (Fig. 11).

ALASKA: Wynne 5148–C, 29.vii.1980, northwest part of Siginaka Islands, Sitka, Baranof Island; epiphytic on *Ralfsia fungiformis* (Gunnerus) Setchell & Gardner. Wynne 5200–A, 27.vii.1980, Three Entrance Bay, Sitka, Baranof Island.

This species is a rare alga previously known only from northwestern Europe (Rosenvinge & Lund 1943; Kylin 1947; Rueness 1977) and Newfoundland, Canada (Hooper & South 1977). The genus *Myriocladia* is characterized by growth from a single monopodially constructed filament with a long intercalary meristem and a distal portion extending as an assimilatory filament. The medulla is organized of several firmly united central filaments, and descending rhizoids are formed peripheral to the central filaments. A clear demarcation separates the central axis from the assimilatory filaments comprising the cortex (Fig. 11). The assimilatory filaments are of uniform appearance, long and cylindrical and are not embedded in mucilage. Phaeophycean hairs are present, but pluricellular sporangia are absent.



FIGS. 9–12. Figs. 9, 10, *Sphacelaria caespitula*; Fig. 11, *Myriocladia lovenii*; Fig. 12, *Acrothrix gracilis*. Fig. 9. Erect axis. Fig. 10. Plurilocular sporangium. Fig. 11. Portion of axis showing clear separation between cortex and medulla. Fig. 12. Herbarium specimen (Wynne 5545). Scale bars: 30 μm in figs. 9, 11; 20 μm in fig. 10.

The Alaskan *Myriocladia lovenii* bears abundant unilocular sporangia, which arise at the bases of the tufts of assimilatory filaments. Thalli are densely branched and attain heights of 20 cm. The reproductive phenology appears to coincide with that of Newfoundland populations, which appear in June, become fertile in late July, and are gone by late August or early September (Hooper & South 1977).

Although Kylin (1947) reported his collections from the Swedish west coast to be only 2–6 cm tall and little branched, Danish specimens were rarely up to 12–13 cm tall and more abundantly branched (Rosenvinge & Lund 1943). Levring (1937) reported his collections, from the west coast of Norway, to reach 25 cm in height and to be richly branched, similar to the Alaskan material. According to Levring the smaller stature results from growth under conditions of reduced salinity, and the more robust habit is achieved under normal salinity.

Previously, only one other species of *Myriocladia* had been reported from the North Pacific, namely, *M. kuromo* Yendo from Japan (Kylin 1940). But that species was later transferred to *Papenfussiella* by Inagaki (1958), because the plants lacked phaeophycean hairs but possessed two kinds of assimilatory filaments, the shorter type being embedded in mucilage. Thus, *M. lovenii* is the sole representative of *Myriocladia* now recognized as occurring in the North Pacific. Other species of *Myriocladia* are known from various parts of the world (Kylin 1940).

ACROTRICHACEAE

Acrothrix gracilis Kylin (Fig. 12).

ALASKA: Wynne 5302, 5309, 8.viii.1980, Cape Suspiro, near Craig, Prince of Wales Island. Wynne 5343, 5359, 9.viii.1980, east side of Heceta Island (55°47'54"N, 133°28'52"W), southern Sea Otter Sound, Prince of Wales Island. Wynne 5545, 5575, 12.viii.1980, west spit of Fish Egg Island, Craig, Prince of Wales Island.

Abundant collections of this species were made. Some specimens have a smooth aspect (Fig. 12), whereas others have a more pubescent aspect. Forward & South (1985) presented evidence that a single morphological taxon of this genus is present in the North Atlantic, namely, *A. gracilis*. Thus, they included within the synonymy of *A. gracilis* two other species previously recognized in the North Atlantic, *A. novae-angliae* Taylor and *A. norvegica* Levr. Levring (1937) stated that the assimilatory filaments in his *A. norvegica* are 7–15 cells long; the primary assimilatory filaments reported by Kylin (1907) in his original description of *A. gracilis* are 7–10 cells long. The number of cells in the assimilatory filaments in the Newfoundland plants was up to 20 (Forward & South 1985). Kawai (1983) reported the occurrence of *A. gracilis* in northern Japan, and he observed the number of cells in the assimilatory filaments to be 7–19. A similar broad range in the number of cells in the assimilatory filaments occurs in Alaskan plants, and this variation seems to be responsible for the smooth to pubescent aspects present. Kawai has also shown that there are two types of assimilatory filaments in this species, symmetric ones more common in upper parts of the thallus and asymmetric ones in the middle and lower parts of the thallus.

A second species of *Acrothrix*, *A. pacifica* Okamura & Yamada, also occurs in the North Pacific. Assimilatory filaments in *A. pacifica* are consistently symmetric irrespective of the part of the thallus (Kawai 1983).

ACKNOWLEDGMENTS

Collections at Amchitka Island were made during the participation of the Fisheries Research Institute of the University of Washington in the U.S. Atomic Energy Commission's projects on the island in 1967–1971. Collections in southeast Alaska were made possible by a grant from the Office of the Vice-President for Research, University of Michigan, in 1980. Sandra C. Lindstrom and Carl Lindstrom provided logistical assistance, which is greatly appreciated. I am also grateful to M. Masuda for his confirmation of my identification of *Neorhodomela aculeata* and to H. Kawai for his discussions on the Chordariaceae.

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